507.73
.P4P6846

MEMOIRS

OF THE

CARNEGIE MUSEUM.

1904-1906.

VOL. II.

W. J. HOLLAND, *Editor*

Smithsonian Institution,
MAR 4 1907
198092
National Museum.

PITTSBURGH.
Published by the Authority of the Board of Trustees of the
CARNEGIE INSTITUTE.

Press of
The New Era Printing Company
Lancaster, Pa.

PREFATORY NOTE.

The publication of the Memoir by Dr. Arnold E. Ortmann upon "The Crawfishes of the State of Pennsylvania," concludes the Second Volume of the Memoirs of the Carnegie Museum.

The paper on "The Osteology of Haplocanthosaurus" by Mr. J. B. Hatcher was the last paper from his pen to appear in the publications of the Museum. He died on July 3, 1904, and the sole responsibility for the supervision of the Memoirs and Annals of the Museum devolved upon the writer, who without any assistance has endeavored to perform the combined task of proof-reader and editor of the publications, a task which, while in some respects pleasant, has laid a great burden upon him, taxed as he has been by the care of several departments of activity in the museum, and the general supervision of the whole.

The pleasurable and consolatory reflection always remains, that by these publications very important additions are being made to the sum of human knowledge.

The first Memoir in Volume IV. upon "Early Chinese Writing" has been published, and the first Memoir in Volume III. upon the Archeology of the Pacific Slope of Costa Rica by C. V. Hartman is in press and shortly will be given to the public.

W. J. Holland.

December 1, 1906.

TABLE OF CONTENTS.

PAGE.

PREFATORY NOTE iii

LIST OF FIGURES IN TEXT vii

LIST OF PLATES ix

MEMOIR I. Osteology of Haplocanthosaurus. J. B. Hatcher . . . 1

MEMOIR II. Osteology of Baptanodon Marsh. C. W. Gilmore . . . 77

MEMOIR III. Fossil Avian Remains from Armissan. C. R. Eastman . . 131

MEMOIR IV. Description of New Rodents. O. A. Peterson . . . 139

MEMOIR V. The Tertiary of Montana. Earl Douglass 203

MEMOIR VI. The Osteology of Diplodocus Marsh. W. J. Holland . . 225

MEMOIR VII. The Osteology of Protostega. G. R. Wieland 279

MEMOIR VIII. New Suilline Remains from the Miocene of Nebraska. O. A. Peterson 305

MEMOIR IX. Notes on the Osteology of Baptanodon. C. W. Gilmore . . 325

MEMOIR X. The Crawfishes of the State of Pennsylvania. Dr. Arnold E. Ortmann 343

Index 525

LIST OF FIGURES IN TEXT.

PAGE.

Diagram of portion of bone-quarry near Canyon City, Colorado, showing positions of *Haplocanthosaurus priscus* and *H. utterbacki* when found 4

Diagram of portion of bone-quarry near Canyon City, Colorado, worked for Carnegie Museum 5

Sixth (?) dorsal of type of *Haplocanthosaurus priscus* seen from right side 10

First Dorsal of *H. priscus* seen from right side 10

Superior view of sacral, anterior caudal, and posterior dorsal, or lumbar, of *Menopoma allegheniensis* 21

Superior view of sacrum, anterior caudal, and posterior lumbar or dorsal of *Iguana tuberculata* 21

Chevron of *Haplocanthosaurus* between caudals 8 and 9, side view 23

Chevron of *Haplocanthosaurus* between caudals, posterior view 23

Chevron of *Haplocanthosaurus* between caudals 13 and 14, side view 23

Chevron of *Haplocanthosaurus* between caudals, posterior view 23

Anterior view of second (?) rib of right side of *Haplocanthosaurus* 24

Anterior view of fourth (?) rib of left side of *Haplocanthosaurus* 24

Anterior view of thirteenth (?) rib of left side of *Haplocanthosaurus* 24

Left femur of *Haplocanthosaurus priscus*, front view 27

Sacrum of *Haplocanthosaurus utterbacki*, seen from right side 36

Anterior view of disarticulated parapophyses (sacral ribs) of *Haplocanthosaurus utterbacki* 36

Posterior view of left scapula of *H. utterbacki* 42

External view of left scapula of *H. utterbacki* 42

External view of right coracoid of *H. utterbacki* 42

Centrum of fourth sacral of *H. utterbacki* seen from right side 51

Scapulæ of *Cetiosaurus longus* Owen 52

Coracoid of *Cetiosaurus longus* Owen 53

Photograph of footprint in Jurassic sandstone, near Canyon City, Colorado 61

Photograph of ripple-marks on surface of Jurassic sandstone, Big Horn Mountains, Wyoming 62

View of Atlantosaurus beds, entrance to Garden Park, near Canyon City, Colorado 63

The "Nipple," showing in foreground trench cut by Professor Cope in collecting Dinosaur remains 64

Eastern entrance to Cope quarry 65

View from near Cope quarry with the "Nipple" in foreground, Cooper Mountain in the distance, Garden Park below the "Nipple" 66

Radius and ulna of *Diplodocus* 73

Supposed clavicle of *Diplodocus* 73

PAGE.
Cross-section of upper and lower jaws of *Baptanodon* 95
Cross-section of lower jaw of *Baptanodon* 95
Internal view of posterior end of left mandibular ramus of *Baptanodon discus* 97
Internal view of left articular of *Baptanodon discus* 98
Anterior view of left articular of *Baptanodon discus* 98
Posterior tooth of *Baptanodon discus* 99
Cross-section of tooth of *Baptanodon discus* 99
Right thyrohyal of *Baptanodon discus* 100
Anterior view of atlas and axis of *Baptanodon discus* 102
Lateral view of atlas and axis of *Baptanodon discus* 102
Posterior view of atlas and axis of *Baptanodon discus* 103
Left half of paired neural arch of atlas of *Baptanodon discus* 104
Superior view of anterior cervical of *Baptanodon discus* 104
Anterior view of anterior cervical of *Baptanodon discus* 104
Cross-section of an anterior dorsal centrum of *Baptanodon discus* 105
Cross-section of dorsal centrum of *Baptanodon discus* 106
Cross-section of posterior dorsal or anterior caudal centrum of *Baptanodon discus* 106
Lateral view of centra from different regions of *Baptanodon discus* 106
End and lateral views of an extreme caudal of *Baptanodon discus* 107
Posterior view of a right dorsal (?) of *Baptanodon discus* 108
Ventral view of pectoral girdle of *Baptanodon discus* as found in matrix 109
Interior view of interclavicle of *Baptanodon discus* 113
Superior view of fore paddle of *Baptanodon marshi* 114
Dorsal view of humerus of *Baptanodon marshi* 115
Left hind (?) paddle of *Baptanodon discus* 115
Atlas, axis, and third and fourth cervical of *Baptanodon marshi* 122
Crown view of superior grinders of *Steneofiber fossor* 141
Crown view of inferior grinders of *Steneofiber fossor* 141
Fore-limb of *Steneofiber fossor* in position 158
Steneofiber barbouri 166
Field sketch of a weathered rhizome containing type of *Steneofiber barbouri* 185
Weathered portion of a Dæmonelix containing skeleton of *Steneofiber fossor* 186
Forms of Dæmonelix 187
Spiral and part of rhizome of Dæmonelix 188
A newly dug Prairie Dog burrow 189
Diagram of cast of an old burrow of Prairie Dog 189
Underground fortress of mole (*Talpa europæa*) 189
Skull and anterior cervical vertebræ of *Diplodocus Carnegiei* Hatcher as placed in restoration at British Museum 228

Page.
Sketch by Miss Alice B. Woodward showing supposable attitude of *Diplodocus* 229
Side view of skull of *Diplodocus* 230
Posterior view of the back of skull of *Diplodocus* 231
Lateral view of posterior portion of skull of *Diplodocus* 233
Superior view of posterior portion of skull of *Diplodocus* 235
Anterior view of posterior part of skull of *Diplodocus* 236
Diagram showing relation of the bones at outer margin of supratemporal fossa of *Diplodocus*. 237
Inferior view of posterior part of skull of *Diplodocus* 241
Posterior view of intercentrum of atlas of *Diplodocus* 247
Anterior view of intercentrum of atlas of *Diplodocus* 247
Inferior view of intercentrum of atlas of *Diplodocus* 247
External view of left neural arch of atlas of *Diplodocus* 247
Internal view of right neural arch of atlas of *Diplodocus* 247
Inferior view of Odontoid 248
Superior view of Odontoid 248
Posterior view of Odontoid 248
Anterior view of Odontoid 248
External, internal and inferior views of supposed rib of atlas of *Diplodocus* in American Museum of Natural History 259
External, internal and inferior views of supposed ribs of axis of *Diplodocus* in American Museum of Natural History 250
Sketch of manner in which the two cervical ribs of *Diplodocus* may have functioned in connection with the atlas and axis 250
Outline drawing of a series of posterior caudal vertebræ of *Cetiosaurus leedsi* Hulke 254
Vertebræ of posterior part of tail of *Cetiosaurus leedsi* Hulke, as exhibited in the British Museum 254
Photograph of the two sternal plates and the supposed clavicles as provisionally and temporarily placed by the author in the restored skeleton in the British Museum 257
Lateral view of the sternal plates and supposed clavicles at British Museum 258
Superior view of pectoral girdle of *Crypotoclidus oxoniensis* 259
Anterior view of pectoral girdle of *Cryptoclidus oxoniensis* 260
The two supposed clavicles of *Diplodocus* 261
Sections of shafts of supposed clavicles of *Diplodocus* 262
Protostega gigas — superior view of skull with lower jaw and hyoid, right anterior border of carapace, and right fore flipper 282
Protostega gigas. Carapace less the nuchal and marginal series, inner view 286
Ental view of a large humerus of *Protostega gigas* 287
Right shoulder and flipper of *Protostega gigas* 288
Right pelvic girdle and flipper of *Protostega gigas* 291

PAGE.
Ungual phalanges of *Protostega gigas* 292
Left front flipper of *Toxochelys latiremis* 293
Fore and hind flippers of *Colpochelys kempi* in the United States National Museum 294
Oblique internal view of left mandible of *Thinohyus* (B) *subæquans* Cope 307
External view of left lower mandible of *Thinohyus* (B) *subæquans* Cope 307
Superior view of left lower mandible of *Thinohyus* (B) *subæquans* Cope 307
Anterior portions of upper and lower jaws of *Thinohyus siouxensis* 317
Internal view of the right mandibular ramus of *Baptanodon natans* 327
Cross-section of posterior end of left mandibular ramus of *Baptanodon natans* 327
Cross-section of sclerotic plates of *B. natans* 328
Lateral view of a section of the anterior part of rostrum of *Baptanodon natans* 329
Cross-section near middle of snout of *Baptanodon natans* 329
Atlas, axis, third and fourth cervical vertebræ of *Baptanodon natans* 330
Lateral view of intervertebral disk of *Baptanodon natans* 330
View of the proximal end of humerus of *Baptanodon natans* 331
Ulna of *Baptanodon natans* 331
Radius of *Baptanodon natans* 331
External view of acetabular end of ilium of *Baptanodon discus* 332
Atlas, axis, third, fourth, fifth and sixth cervical vertebræ of *Baptanodon robustus* 333
Lateral view of anterior or median dorsals of *Baptanodon robustus* 334

LIST OF PLATES.

PLATE.
I. Presacral Vertebræ of Type of *Haplocanthosaurus priscus.*
II. Vertebræ of Type of *Haplocanthosaurus utterbacki.*
III. Nineteen Anterior caudals of *Haplocanthosaurus priscus.*
IV. Pelvis of *Brontosaurus ;* Pelvis of *Diplodocus ;* Pelvis of *Haplocanthosaurus.* All seen from left side.
V. Inferior, Anterior and Posterior views of Pelvis of *Haplocanthosaurus priscus.*
VI. Restoration of *Diplodocus carnegiei.*
VII. Diagram showing Position in which the Elements of the Specimen of *Baptanodon discus* Marsh were found Imbedded in Concretion.
VIII. Side view of Skull of *Baptanodon discus* Marsh.
IX. Skull of *Baptanodon discus.*
X. Side view of Skulls of *Baptanodon discus.*
XI. Posterior Views of the Skull of *Baptanodon discus.*
XII. Anterior, Dorsal, and Ventral Views of Pectoral Girdle of *Baptanodon discus.*
XIII. *Taoperdix keltica* Eastman.
XIV. *Taoperdix keltica* Eastman. Restoration.
XV. *Taoperdix pessieti* (Gervais).
XVI. *Taoperdix pessieti* (Gervais).
XVII. Fossil Rodents from the Upper Miocene, Harrison Beds.
XVIII. Fossil Rodents from the Upper Miocene, Harrison Beds.
XIX. Restoration of *Steneofiber fossor.*
XX. Mounted skeleton of *Steneofiber fossor.*
XXI. Microscopic Sections of Cellular Structures in Dæmonelix.
XXII. Lower White River Mammals. Ictops and Xenotherium.
XXIII. Side view of Skulls of *Diplodocus longus* Marsh, Preserved in the United States National Museum.
XXIV. Top view of Skulls of *Diplodocus longus* Marsh, Preserved in the United States National Museum.
XXV. Back view of Skulls of *D. longus* Marsh, United States National Museum.
XXVI. Photograph of Skull of *Diplodocus* Preserved in the American Museum of Natural History.
XXVII. Posterior and Anterior View of Back Part of Skull of *Diplodocus.*
XXVIII. Superior view of Back Part of Skull of *Diplodocus.*
XXIX. Posterior Caudal Vertebræ of *Diplodocus carnegiei* Hatcher.

PLATE.
XXX. Restoration of the Skeleton of *Diplodocus carnegiei* Hatcher.
XXXI. *Protostega gigas* Cope. Shoulder Girdles, Pelvic Girdle, Hyoids.
XXXII. *Protostega gigas* Cope. Forearm, Hand, and Foot.
XXXIII. *Dermochelys coriacea.*
XXXIV. *Thinohyus siouxensis* Peterson. Right side of Skull and Lower Jaws and Superior View of Mandible.
XXXV. Superior and Palate Views of skull of *Thinohyus siouxensis* Peterson.
XXXVI. Side View of Skull of *Baptanodon discus* Marsh.
XXXVII. Superior and Inferior Views of *Baptanodon discus.*
XXXVIII. Pectoral Girdle of *Baptanodon robustus.*
A. *Cambarus obscurus, C. diogenes,* and *C. carolinus* reproduced by the three-color process.
B. *Cambarus bartoni, C. bartoni robustus, C. limosus,* and *C. monongalensis,* reproduced by the three-color process.
XXXIX. Anatomical details of structure of Pennsylvanian Cambari.
XL. Chelæ of Pennsylvanian Cambari and burrows of *D. bartoni* and *C. carolinus.*
XLI. Burrows of Pennsylvanian Cambari.
XLII. Preglacial Monongahela River, and present range and distribution of species.
XLIII. Map of Pennsylvania showing distributional areas of crawfishes.

OSTEOLOGY OF HAPLOCANTHOSAURUS,

WITH

DESCRIPTION OF A NEW SPECIES,

AND

REMARKS ON THE PROBABLE HABITS OF THE SAUROPODA AND THE AGE AND ORIGIN OF THE ATLANTOSAURUS BEDS.

BY J. B. HATCHER.

ADDITIONAL REMARKS ON DIPLODOCUS.

BY J. B. HATCHER.

[Reprinted from MEMOIRS CARNEGIE MUSEUM, Volume II., No. 1, November, 1903.]

PRESS OF
THE NEW ERA PRINTING COMPANY,
LANCASTER, PA.

187744

OSTEOLOGY OF HAPLOCANTHOSAURUS,[1] WITH DESCRIPTION OF A NEW SPECIES, AND REMARKS ON THE PROBABLE HABITS OF THE SAUROPODA AND THE AGE AND ORIGIN OF THE ATLANTOSAURUS BEDS.

By J. B. Hatcher.

The present paper is the third of a series of memoirs based on the fossil vertebrata in the collections of the Carnegie Museum. These memoirs, prepared either directly by the curator of the Department of Vertebrate Paleontology, by his assistants, or others under his general direction, will continue to appear at irregular intervals. Their chief purpose will be to describe in detail and to illustrate with fidelity some of the more important fossil skeletons in the collections. While in every instance these papers will be based on material belonging to the collections of the Carnegie Museum, for the sake of completeness, wherever other and supplementary material is accessible in the collections of other museums it will be utilized and the fullest credit will, in all such instances, be given for such favors. The precarious conditions attending the preservation, fossilization, and final recovery of the skeletons of extinct vertebrates have necessarily been such as to render the occurrence of really complete skeletons conspicuously rare. This is especially true of the gigantic Sauropoda, and notwithstanding the very large collections in several of our leading museums, it is still possible to determine anything like the complete osteology of the different genera only by selecting the best preserved skeleton of each as a basis and supplementing this from material pertaining to the same genus but to other skeletons and belonging to the same or other museums. Owing to the cordial relations at present existing between the various museums of this country, aided by the exceptional energy with which a few institutions are increasing their collections our knowledge of the structure and relations of a considerable number of known dinosaurian genera has been materially increased during the past few years, while occasional discoveries of entirely new forms have been announced.

---

[1] Proc. Biol. Soc. Wash., Vol. XVI., 1903, pp. 1 and 2, and p. 100.

It appears somewhat remarkable however that a Sauropod dinosaur of such gigantic size and showing such distinctive generic characters as does *Haplocanthosaurus* should have been discovered so recently at the exact locality, near Canyon City, Colorado, so long worked and rendered classic by the researches of the late Professor Othniel Charles Marsh. This discovery may be taken as an indication not only of the great wealth of this particular locality in the remains of the Dinosauria but of the great diversity that existed in the reptilian life of this region in Jurassic times. For since this single bone quarry, restricted in area to a few hundred square feet and with the bone-bearing horizon not more than three feet thick vertically, has already produced representatives of at least a dozen genera and species and twice or thrice that number of individual skeletons it would seem difficult to overestimate the wealth of the reptilian fauna of this region in Jurassic times or to exaggerate the total number of genera and species that must have existed throughout the period of time required for the deposition of the several hundred feet of sandstones and shales that here constitute that formation and imbedded within which we may still hope to find remains of additional genera and species pertaining to that peculiar but long since extinct group, the Dinosauria.

For the material upon which the present paper is based we are indebted first of all to the generosity of Mr. Andrew Carnegie whose munificence made it possible to carry on the excavations necessary for its recovery. To the skill, energy and patience however of Mr. W. H. Utterback we are directly indebted for its recovery from the hard, almost granitic sandstones in which the bones lay buried beneath many feet of other sandstones and shales only a little less refractory than those actually containing the fossils. After these superincumbent sandstones and shales had been removed over a considerable area the actual and more difficult work of developing and recovering the fossil bones was begun. These, as has been stated above, lay buried in a thick stratum of heavily bedded and hard sandstone. Not only was this sandstone for the most part extremely hard but it was also considerably fractured in such manner as greatly to increase the difficulty encountered in taking up the bones in a proper manner. All difficulties were however met and overcome by Mr. Utterback with commendable patience and ingenuity, and the different blocks were received at the paleontological laboratory of the museum with all the vertebræ and other bones in each block still in their original positions relative to one another. While aided by diagrams of the quarry, reproduced here in Figs. 1 and 2, and the proper marking of each block as it was taken up, it is now easily possible to assign the different blocks to their proper position in the quarry and thus to determine with accuracy the relative positions of all the different bones as they lay imbedded in the rock.

In the laboratory the bones have been very carefully and skillfully freed from the matrix under the direction of Mr. Arthur S. Coggeshall as Chief Preparator assisted by Messrs. W. H. Utterback, L. S. Coggeshall and A. W. VanKirk.

When freed from the matrix the bones were all faithfully drawn by Mr Sydney Prentice, draughtsman in the Paleontological Department of this Museum.

The type No. 572 of the present genus consists of the two posterior cervicals, ten dorsals, five sacrals, nineteen caudals, both ilia, ischia and pubes, two chevrons, a femur and a nearly complete series of ribs, all in an excellent state of preservation and pertaining to an individual fully adult as is shown by the coössified neural spines and centra.

Position of the Different Bones as they Lay Imbedded in the Quarry.

The pelvis, sacrum, left femur and nineteen anterior caudals were the first portions of the skeleton discovered. They lay in the position shown at *A*. 572 in the diagrams of the quarry shown in Figs. 1 and 2. The ilia, ischia and pubes still occupied approximately their normal positions relative to the sacrum, and the femur was directed backward and downward, with the head removed about two feet from the acetabulum. The anterior caudal was displaced from its normal position relative to the distal extremity of the sacrum, but the succeeding eighteen caudals were interlocked by their zygapophyses. The two chevrons lay as shown in the diagram, approximately in position, with caudals eight and thirteen. I personally assisted in taking up this portion of the skeleton and am therefore somewhat familiar with its appearance as it lay in the quarry.

At a distance of about twelve feet but on the same level as the pelvis and bones above mentioned, were found the nine posterior dorsal vertebræ shown at *B*. 572 in the diagrams of the quarry. These were all interlocked by the zygapophyses and most of the ribs were still in place. The last of this series agrees very well in size and general appearance with the first sacral of the series found at *A*. 572, and there would seem no good reason for assuming that the two series pertain to other than one and the same skeleton, though, of course, this cannot be absolutely demonstrated, but the characters exhibited by the two series demonstrate that they pertain to the same species at least and I have little doubt but that they belong to the same individual.

With the ninth from the posterior of this series of vertebræ there was an interruption, and the three vertebræ shown at *C*. 572 were found closely adjacent to the anterior of the nine dorsals mentioned. These three vertebræ were interlocked by their zygapophyses and consist of the first dorsal and the last two cervicals. They evi-

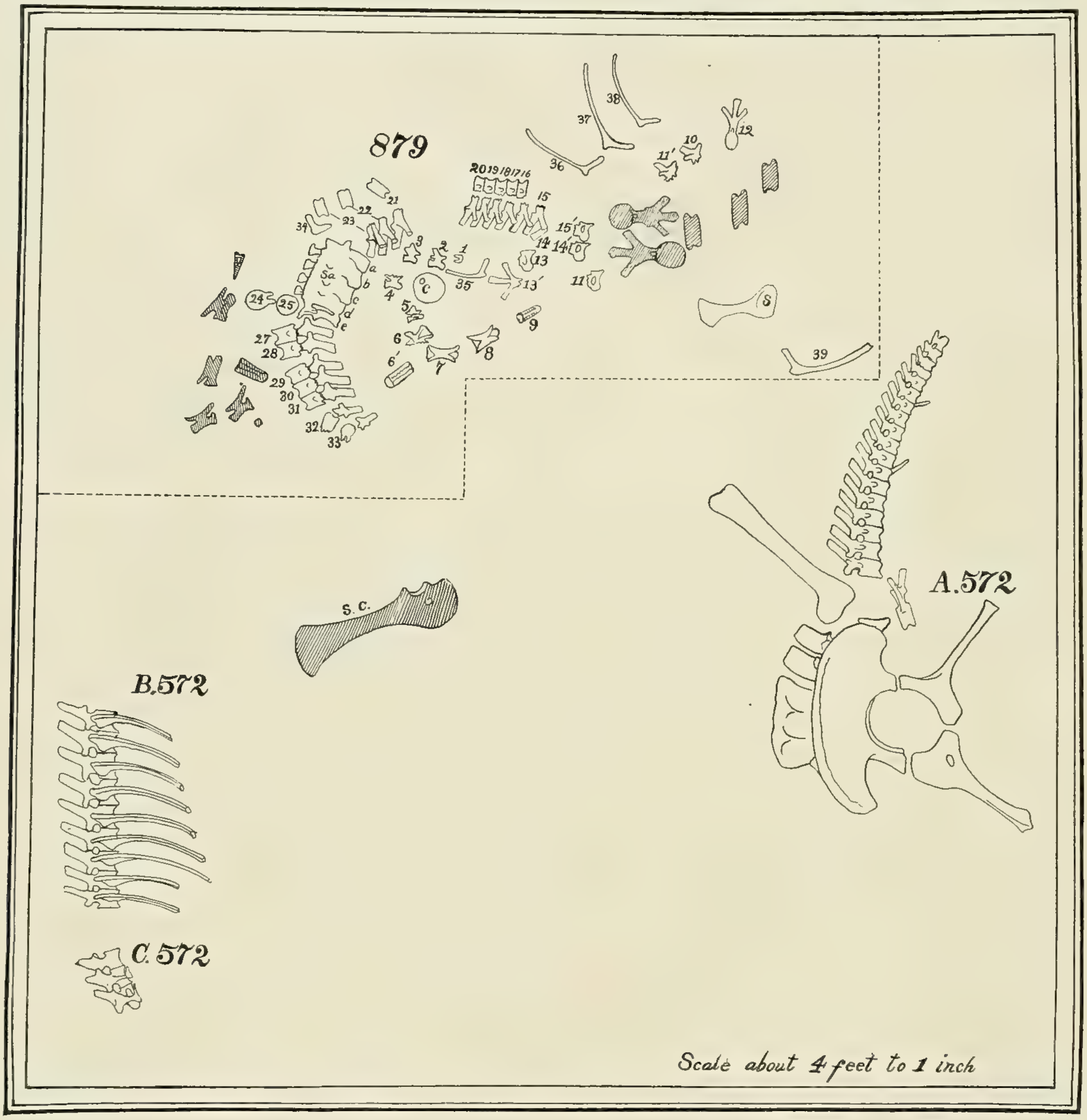


FIG. 1. Diagram of west end of that portion of bone quarry near Canyon City, Colo., worked by W. H. Utterback, showing the positions in which the types of *Haplocanthosaurus priscus* (No. 572, *A*, *B*, *C*) and *H. utterbackii* (No. 879) were found. The shaded bones pertain to a different genus. *A*. 572 femur, pelvis, sacrum and nineteen anterior caudals; *B*. 572 nine posterior dorsals; *C*. 572 first dorsal and last two cervicals.

dently pertain to the same series as the nine dorsals and the differences in the spines, positions of the rib facets, etc., demonstrate that a number of dorsals are missing between this first dorsal and the anterior of the series of nine posterior dorsals; while the remains of a second skeleton pertaining to a different species of the same genus fixes the number of missing dorsals at four. This would place the number of free dorsals in the present genus and species at fourteen instead of ten, the probable number in *Diplodocus* and *Morosaurus*. It is possible, however, that in the Dinosauria the number of dorsals may vary in different individuals within the same species as is well known to be the case in numerous instances in the Mammalia.

The bones within the dotted lines in the upper left-hand corner of the first diagram (Fig. 1) for the most part pertain to and constitute the type of a new species of *Haplocanthosaurus*, which will be described later in this paper. The shaded bones within the dotted lines and the scapula and coracoid beneath pertain to one or more genera different from *Haplacanthosaurus*. The relative positions of these bones as they lay imbedded in the sandstones are well shown in the diagrams and will be referred to in detail, when we come to describe the species of which they form the type.

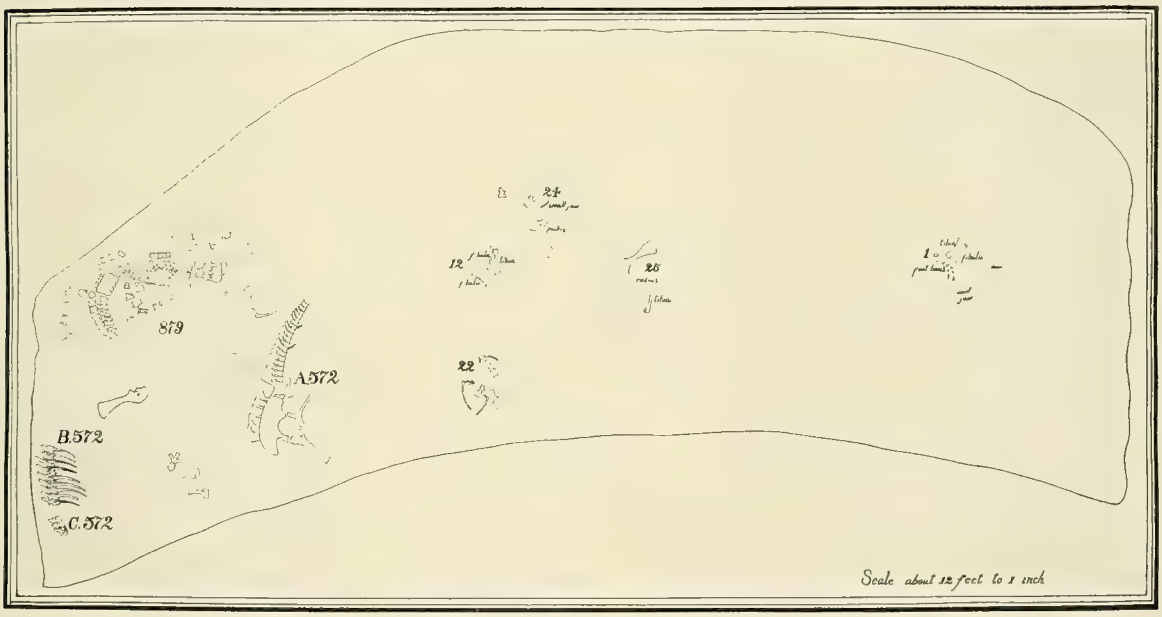


FIG. 2. — Diagram of that portion of bone quarry near Canyon City, Colo., worked by Mr. W. H. Utterback for Carnegie Museum. The lower irregular line shows limit to which quarry had been worked by the late M. P. Felch for Professor Marsh.

The quarry from which these remains were recovered is the one long worked by Professor Marsh. It is situated on the west side of Oil Creek (Four Mile Creek) at the entrance to Garden Park and some nine or ten miles east by north of Canyon

City, Colorado. The horizon is in the Jurassic[2] and some 100 to 150 feet above the summit of the red Triassic? sandstones. It is I believe a decidedly lower horizon than the dinosaur beds near Morrison, Colo.; Como, Little Medicine Bow and Sheep Creeks, Wyoming or Piedmont, South Dakota.

In the diagram of the quarry shown in Fig. 2 the bottom line shows the limit to which the quarry had been worked by Professor Marsh while the area above this line is that worked by Mr. Utterback for the Carnegie Museum.

Description of the Type (No. 572) of Haplocanthosaurus Priscus.

The Vertebræ.

The Cervicals (Plate I., Figs. *C* 15 and 14).—Only the last two cervicals were recovered. Fortunately these, together with the first dorsal, were still interlocked by their zygapophyses and thus the actual position of these three vertebræ in the vertebral column can be definitely determined. They were somewhat crushed and distorted, but considering the hard and fractured nature of the sandstone in which they were imbedded they are in a very good state of preservation and remarkably complete. These vertebræ are rather low, broad and short for the posterior cervicals of a Sauropod dinosaur of such dimensions as is indicated by the remains of the present skeleton and suggest a reptile with a neck which, though, of moderate length, was decidedly more abbreviated than was that of *Diplodocus*, a contemporaneous but more highly specialized Sauropod.

The Fourteenth? Cervical (Plate I., Fig. *C* 14).—Assuming that there were the same number of vertebræ in the cervical series of *Haplocanthosaurus* as in *Diplodocus*, the first of the series of vertebræ now under consideration would correspond to the fourteenth cervical. It is not improbable, however, that the number of cervicals in the present genus was less than in *Diplodocus*. Hence, I have interrogated the numerical position of this vertebra in the cervical series, although as already stated, there can be no doubt of its being the last but one of that series.

The centrum is strongly opisthocœlous and with the transverse diameter exceeding the vertical, though these dimensions have doubtless been somewhat altered by pressure. The sides of the centrum are invaded by long and deep pleurocentral cavities[3] separated only by a thin median septum. These cavities are extended forward into the base of the ball of the centrum while posteriorly they are only separated by a thin plate of bone from the cavity for the ball of the succeeding vertebra.

---

[2] By some considered as Lower Cretaceous.

[3] For an explanation of the names applied to the various cavities, laminæ, etc. of the Sauropod vertebræ, see the author's paper on Diplodocus, Mem. Car. Mus., Vol. I., No. 1, pp. 16–19.

In this manner the centrum of the vertebra is reduced to superior and inferior horizontal plates united by a vertical median septum or plate. At the posterior extremity these plates expand into a deeply excavated disk which forms the cup for the succeeding vertebra while at the anterior extremity they unite to form the ball of the centrum. A cross-section of the centrum midway between the anterior and posterior extremities is irregularly I-shaped and somewhat suggestive of that of an I beam in structural materials. The inferior surface of the centrum is broad and flat, much expanded posteriorly and moderately expanded anteriorly where at a point a little back of the ball it gives rise to the cervical rib. The cervical rib is firmly coössified both with the centrum below, through the intermedium of a parapophysis, and with the diapophysis above. There is a short anterior branch of the cervical rib and a longer posterior one. The latter stops short of the posterior extremity of the centrum. It is proportionately broader and stronger than in *Diplodocus carnegii* but decidedly shorter and less robust than in *Brontosaurus excelsus.*

Seen in front this vertebra appears rather low, with broadly expanded cervical ribs and prezygapophyses. There is a single supraprezygapophysial cavity and two infraprezygapophysial cavities separated by a median septum formed by the union of the horizontal laminæ of opposite sides and supported below by the superior wall of the neural canal. In the vertebra under consideration the greater portion of this septum has been lost. It is restored in plaster, and in the drawings the restored parts are indicated by broken lines in the shading. As shown in the drawings the neural spine is also absolutely simple instead of deeply bifurcated as are the spines of the vertebræ of this region in all other known genera of Sauropod dinosaurs wherever it has been possible to determine their character. The neural canal is rather large as compared with that in *Diplodocus.*

Seen from the rear the neural canal is nearly circular and appears as if sunk into the superior surface of the centrum. The postzygapophysial laminæ each send forward a broad thin plate. These unite with the neural spine and enclose a very deep suprapostzygapophysial cavity while below as in front there are two small but deep infrapostzygapophysial cavities separated by a median septum.

The diapophyses are only moderately expanded and they are braced anteroposteriorly by the horizontal laminæ and inferiorly by the inferior branches of the diapophysial laminæ which are very short and almost perpendicular. There is no superior branch of the diapophysial lamina. The posterior branch of the horizontal lamina runs obliquely upward and backward from the diapophysis to the posterior zygapophysis, thus giving additional support to the latter element. Another lamina, horizontal in position but homologous with one of the oblique laminæ, runs directly backward from the diapophysis nearly to the posterior border of the centrum. There are deep and well-defined post-, pre-, supra- and infradiapophysial cavities.

The Fifteenth? or last Cervical (Plate I., Fig. *C* 15). — This vertebra differs from the one preceding it in being a little shorter and with more widely expanded neural spine and cervical ribs. The pleurocentral cavity is less extended posteriorly than in the preceding cervical and its bottom is interrupted by an oblique and an intersecting lamina. There is a shallow infracentral cavity on either side of the median line on the inferior surface near the anterior end of the centrum. There is a single infraprezygapophysial cavity. The neural spine is absolutely simple as in the preceding cervical. The postzygapophyses are higher and the posterior branch of the horizontal lamina consequently more nearly vertical than in the preceding vertebra. The anterior branch of the horizontal lamina has the margin somewhat expanded as shown in Plate I., Fig. *C* 15, indicating that this vertebra gave some support to the scapula.

The First Dorsal (Plate I., Fig. 1). — Fortunately as has already been stated this vertebra and the two preceding were still closely interlocked by their zygapophyses when discovered in the quarry. They were taken up in a single block of the enclosing sandstone and were received at the musenm still occupying their original positions relative to one another. In consideration of these facts there can be no question regarding the exact position of these three vertebræ in the vertebral column. That the vertebra now under consideration was a dorsal is conclusively shown not by the presence of tubercular and capitular rib facets showing that it supported on either side a free rib, for there are in our collections of sauropods, skeletons of other dinosaurs fully adult but, with the posterior cervical, bearing free cervical ribs articulating by both tubercular and capitular facets as do the ribs of the dorsal region. The character in this vertebra distinguishing it as a dorsal is the broadly expanded external border of the anterior branch of the horizontal lamina. This element has been thus modified in this and the succeeding dorsal, no doubt, as is known to be the case in *Diplodocus* to give greater surface for the attachment of the powerful muscles necessary for the support of the scapula. That this was the first and not the similarly modified second dorsal is conclusively demonstrated by the fact that it was found interlocked by its zygapophyses with the last cervical.

This vertebra is essentially complete, although the form of the centrum has been considerably altered by crushing. In the accompanying drawings this distortion has been eliminated as much as possible. The length of the centrum is noticeably less than that of the last cervical and the antero-posterior diameter of the pleurocentral cavity is greatly shortened. The floor of this cavity is interrupted by neither oblique nor intersecting laminæ. There is no infracentral cavity. The capitular rib facet is nearly circular and slightly pedunculate. Its position is beneath the anterior border of the pleurocentral cavity.

The neural arch is decidedly higher than in the posterior cervicals. The diapophyses are more widely expanded and support at their extremities small triangular tubercular rib facets which face outward and a little downward. These rib facets are not pendant as they are in this and the two succeeding dorsals in *Diplodocus.* The anterior and posterior zygapophyses are both somewhat more elevated than the diapophyses and they are supported laterally by the anterior and posterior blades of the horizontal laminæ which are subequal and unite at an obtuse angle to form and give support to the transverse process or diapophysis. Throughout about two thirds of its length the external margin of the anterior blade of the horizontal lamina presents a greatly expanded rugose surface, which no doubt served for the muscular attachment of the scapula. From below, the transverse process is supported by the short, rather slender inferior blade or branch of the diapophysial lamina which runs obliquely downward and forward to unite with the superior branch of the prezygapophysial lamina, while an extended and powerful oblique lamina runs obliquely downward and backward, uniting with the lateral wall of the neural arch and giving additional support to the transverse process. The pre-, infra- and postdiapophysial cavities are all deep and well enclosed, while the supradiapophysial cavity is shallow and left open anteriorly.

Seen from in front this vertebra appears low with the transverse processes, zygapophyses and neural spine greatly expanded. The neural spine is low and extremely broad. The apex on one side is injured. It is quite simple, not at all bifurcated and with a broad, rugose, median surface. The anterior aspect of the spine is strongly convex transversely throughout its entire length. The articular surfaces of the anterior zygapophyses are elliptical in outline, with the transverse diameter the greater. Between the anterior zygapophyses there extends a thin lamina having the appearance of a broad shelf or platform. Inferiorly the zygapophyses are supported by the powerful inferior branches of the prezygapophysial laminæ while the superior branches of these laminæ are rudimentary. The infrazygapophysial cavity is deep and simple, the supra- is quite shallow.

Posteriorly there is a deep cup on the centrum for the reception of the ball of the succeeding vertebra. The articular surface of the posterior zygapophysis faces downward and outward.

The postzygapophysial laminæ are branched, the internal and smaller of these branches from the zygapophyses of the opposite sides meet in the middle line and form a widely open V. The supra- and infrapostzygapophysial cavities are very deep and at the bottom the latter is subdivided into three unequal pockets by two short, delicate laminæ. On the posterior surface of the neural spine there is a median rugose surface suggestive perhaps of a postspinal lamina.

As has already been remarked, the series of vertebræ was interrupted at the first dorsal and a number of the succeeding vertebræ are missing from the series. I have estimated the number of missing dorsals at four, the second, third, fourth and fifth. If this estimate is correct, and there are many reasons for believing that it is, as will appear later, the first dorsal of the series of nine mentioned above as pertaining to this skeleton would be the sixth of the dorsal series. That these two series of vertebræ pertained to one and the same skeleton is demonstrated beyond the possibility of a reasonable doubt, not alone by their proximity to one another in the quarry where they lay imbedded in the sandstone as shown in Figs. 1 and 2 at *B.* 572 and *C.* 572, but by the relative sizes of the vertebræ, their color and texture and the entirely closed sutures of the neural arches, indicating in each instance an animal of identically the same age.

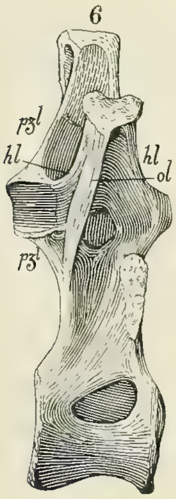


FIG. 3.

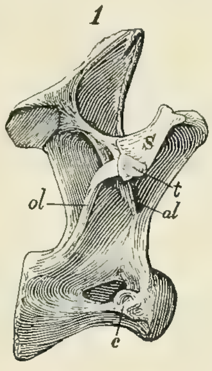


FIG. 4.

FIG. 3. Sixth (?) dorsal of type of *Haplocanthosaurus priscus* (No. 572) seen from right side, $\frac{1}{10}$ natural size, *pzl,* postzygapophysial lamina; *hl,* horizontal lamina; *ol,* oblique lamina.

FIG. 4. First dorsal of same, same view; *ol,* oblique lamina; *al,* inferior blade of diapophysial lamina; *t,* tubercular rib facet; *c,* capitular rib facet; *S,* surface for muscular attachment of scapula, $\frac{1}{10}$ natural size.

Figs. 3 and 4 are side views respectively of the supposed sixth and the first dorsal. They are introduced here for direct comparison with one another and to show the great disparity in structure existing between these two vertebræ. These differences become more apparent after an examination of plate *A*, where posterior and anterior views of the same vertebræ are also given.

The greatest structural differences exhibited in these two vertebræ are to be found in the relative height of the neural arches, the form and position of the capitular rib facets, the form and positions of the transverse processes and the height and form of the neural spine. All these and many other differences of only less importance will become apparent as we describe the sixth dorsal in detail.

Sixth ? Dorsal (Plate I., Fig. 6). — This vertebra is complete save a small part of the anterior end of the centrum and a portion of the upper part of the neural spine. The entire length of the spine is represented, but the margins, except the posterior, are weathered away and have been restored in plaster. It thus happens that the drawing represents the top of the spine less complete than it actually is.

The centrum was opisthocœlous with the cup moderately deep and the ball at the anterior extremity rather more convex than represented in the drawings It is constricted medially, both laterally and inferiorly, and the inferior surface presents a broad median longitudinal ridge. There are no infracentral cavities. The pleurocentral cavities are large, irregularly triangular in outline and very deep, with the dividing median septum reduced to a thin lamina.

The neural arch is high, much constricted transversely and much shorter anteroposteriorly than the centrum. On the anterior lateral margin of either side it supports an elongated, sessile, capitular rib facet situated midway between the anterior zygapophyses and the superior border of the centrum. This facet is quite unlike that of the succeeding dorsals, it is very distinctive and is most like that of the sixth dorsal in *H. utterbackii* to be described later, as compare Plates I. and II.

The transverse processes are high and directed obliquely upward and outward at an angle of about forty-five degrees. At their extremities they bear tubercular rib facets which face outward and a little upward. Inferiorly the transverse process is supported by a powerful lamina arising from the posteroexternal border of the neural arch and forming the greater portion of the broad posterior surface of the transverse process. Although this lamina occupies a position identical with that of the inferior blade of the *diapophysial lamina* in the corresponding dorsal of *Diplodocus*, nevertheless it is clearly homologous with the *oblique lamina* of the first dorsal of this skeleton. In this vertebra the *diapophysial lamina*, only the inferior branch of which is represented in the last cervical and first dorsal described above, has become quite obsolete. There is, in *Haplocanthosaurus*, no division of the anterior blade of the horizontal lamina into superior and inferior branches such as has been shown to be the case in the anterior dorsals of *Diplodocus carnegii.* This fact at once distinguishes that lamina marked *al* and *dl*, in the first dorsal and last cervical as the diapophysial and that marked *ol*, as an oblique lamina, though in no sense to be considered as homologous with the oblique lamina that in the middorsals of *Diplodocus carnegii* gives support posteriorly and inferiorly to the capitular rib facet.

The anterior blade of the horizontal lamina is long and broad, the posterior short and narrow. There is a short and narrow superior blade of the diapophysial lamina invading the bottom of the deep supradiapophysial cavity shown at *dl*, in

Plate I., Fig. 6, second column, and a little anterior to this is a second lamina *al*, which may be an anterior branch of the superior blade of the diapophysial lamina, but which is interpreted as a branch of the prespinal.

Although the transverse process appears massive it is really very light and thin, and save toward the base it is made up entirely of the anterior blade of the horizontal lamina and the oblique lamina. These two laminæ meet at nearly right angles so as to enclose a very deep trough which opens downward, forward and outward and is confluent with the very deep infradiapophysial cavity. There is no prediapophysial cavity and the postdiapophysial cavity is very shallow and inconspicuous.

Seen from in front, the neural arch appears high and constricted just beneath the capitular rib facets but expanded in the region of the superior border of those surfaces. The anterior zygapophyses are elevated and have the articular surfaces elongated transversely and abbreviated antero-posteriorly. Beneath the anterior zygapophyses there is a deep infraprezygapophysial cavity confluent with a deep trough into which the neural canal opens. The supraprezygapophysial cavity is shallow and separated from the one below by a short, stout, transverse plate which gives support superiorly to the lateral borders of the neural arch. In cross-section the neural spine is triangular with the apex of the triangle directed forward and forming the rather broad and rugose prespinal surface.

Seen from behind, the neural spine is broad and rugose, though much narrower than in the first dorsal. This is due to the greater development of the superior blades of the postzygapophysial laminæ, which are thin and expanded and continue to the summit of the neural spine. There are shallow supra- and infrazygapophysial cavities and the latter is much elongated and inclosed laterally by the inferior blades of the postzygapophysial laminæ. These give support inferiorly to a well-formed hyposphenal process developed on this and the succeeding dorsals showing that in addition to the ordinary zygapophysial articulation of the preceding vertebræ the dorsals of this region had a hyposphene-hypantrum articulation.

Dorsals Seven? to Fourteen? Inclusive (Plate I., Figs. 7–14). — After the above rather tedious detailed description of the posterior cervicals and dorsals one and six?, the succeeding dorsals may best be described together. Since, in their more important and general characters, they agree very well both with one another and with the supposed sixth dorsal just described, the following description may very well be limited to a general reference to those characters wherein they all agree, followed by a special reference to the more important distinctive characters of each, wherever such exist. As already stated, these vertebræ, together with the one last described when discovered in the quarry near Canyon City, Colorado, were all closely interlocked by their zygapophyses. They were taken up in a single block of matrix and were received at the museum still imbedded in the sandstone and in their exact original position relative to one another. Thus whatever question there may be regarding their position relative to the last cervical, there can be absolutely no question regarding their position relative to each other, while the same can be said with only a little less certainty regarding their position in relation to the sacrum, for the supposed fourteenth or last of this series, although removed some ten feet from the sacrum, agrees very well in size with the first sacral and has the posterior extremity modified for articulation with that vertebra. There can be no reasonable doubt but that these dorsals and cervicals formed part of the same skeleton as that to which belonged the pelvis and caudals shown in Plates III., IV., V., and the femur shown in text Fig. 14.

In the dorsals now under consideration, the centra are comparatively small, constricted medially, opisthocœlous throughout, though less decidedly so in the posterior region. They are subequal in length, with those of the posterior region a little shorter than those of the anterior. The pleurocentral cavities are deep and subequal in area. They are all irregularly ovate in outline with the broader end directed anteriorly. The neural arches are high and the neural spines short and stout. There is a striking contrast in the proportionate length of the neural spines and height of the neural arches in the dorsals of *Haplocanthosaurus* when compared with those elements in the same vertebræ of any other genus of Sauropod dinosaur known to the present writer. This contrast is especially noticeable in *Diplodocus and Brontosaurus* but is less marked in *Morosaurus.* The capitular facets are somewhat pedunculate and gradually assume a more elevated position in the anterior dorsals until the eighth is reached when they attain an elevation equal to that of the anterior zygapophyses. In the eighth and succeeding dorsals their position remains constant. The transverse processes throughout the entire series of vertebræ now under consideration are subequal in length and are directed upward and outward at an angle of about forty-five degrees. The transverse processes of the posterior dorsals are somewhat more slender than are those of the anterior dorsals. Commencing with the eighth dorsal the superior blade of the diapophysial lamina becomes very well developed and in this and the succeeding vertebra it unites, about midway up the spine, with the superior blade of the postzygapophysial lamina to form a single lamina giving lateral support to the neural spine. The posterior position of the extremity of the transverse process in the eighth dorsal as shown in Plate I., Fig. 8, is due to distortion and is not the normal position of that element. In the seventh and succeeding dorsals the antero-posterior diameter of the neural spines exceeds the transverse and the extremities of all these vertebræ are somewhat expanded and rugose. All the dorsals of this region exhibit the hyposphene-hypantrum articulation.

The Sacrum (Plates IV. and V.). — In the present skeleton as in all other fully adult Sauropod dinosaurs to whatsoever known genus or species they may pertain, there are five vertebræ, coössified by their centra and functioning as sacrals by giving support to the ilia either by means of so-called sacral ribs or transverse processes or by both these elements. Whether or not all five of these vertebræ should be regarded as true sacrals must remain very largely a matter of individual opinion. This matter has already been discussed at some length by the present writer in his paper on *Diplodocus* which formed the first of a series of memoirs, which will continue to appear from time to time relating to the dinosaur remains in the collections of this museum.

Whether the number of true sacrals in the Sauropoda be five or less it is evident that in those genera of American Sauropods where the complete sacrum is known, namely, *Diplodocus*, *Brontosaurus*, *Morosaurus* and *Haplocanthosaurus*, the number of vertebræ functioning as sacrals, that is giving support to the ilia, is constant and is in no sense different in or diagnostic of the several genera as was supposed by the late Professor Marsh. It frequently happens in the case of isolated sacra pertaining to young individuals that one or two of the functional sacrals through not having been firmly coössified with the three vertebræ which, according to the present writer's opinion, constitute the true sacrals, have become detached and lost and in this manner the number of functional sacrals has been mistakenly reduced to either three or four according as the number of detached vertebræ was one or two. By an unfortunate circumstance this proved to be the case with the sacra of *Diplodocus* and *Morosaurus* first discovered and described by Marsh. The sacrum of the first of these genera was found detached and consisted of three coössified centra, while in that of the second (the type of *M. grandis*) there were four coössified centra From these circumstances Professor Marsh quite naturally concluded that the number of functional sacrals in these genera was respectively three for the former and four for the latter and proceeded to make those numbers diagnostic of the genera and families to which they pertained. Subsequent discovery of more complete material has demonstrated beyond a doubt the number of functional sacrals to be five in each of these genera as in *Brontosaurus*. The fragmentary sacra of *Apatosaurus* and *Atlantosaurus* figured by Marsh are evidently incapable of furnishing any definite proof as to the exact number of sacrals in those genera, which should they finally prove to be valid will doubtless also be found to be provided with five functional sacrals. The same remark also applies to the recently described genus *Brachiosaurus* of Riggs. On the other hand it sometimes happens in the skeletons of very old individuals that an anterior caudal or posterior dorsal becomes coössified with the functional sacrals. As an example of the latter the sacrum of the type of *Brontosaurus excelsus* Marsh may be cited. In such instances however there is no danger of misinterpreting the additional vertebræ since they never bear so-called sacral ribs ribs or give any support to the ilia.

The sacrum in the present genus and species may be described in general as being broad, low, with short neural spines and consisting of five vertebræ with subequal, coössified centra. All five of these vertebræ bear parapophyses (sacral ribs) and give support to the ilia through the intermedium of these and the diapophyses. The parapophyses of the three median or true sacrals expand distally and unite to form the inner superior border of the acetabulum as is well shown in Plate V., Fig. 1.

Seen from below (Plate V., Fig. 1) the sacral centra appear subequal in length, with the transverse diameter of the first and last exceeding that of either of the three median or true sacrals. All five of these vertebræ bear so-called sacral ribs springing directly from the middle of the centra, save that of the first, which springs from the superior internal border of the centrum. The excellent state of preservation in which this sacrum was found, firmly attached to the ilia of either side, demonstrates beyond a doubt the fact that all five of the vertebræ bear those processes which have been called sacral ribs. As to whether or not the first of the sacrals is homologous with that which in *Diplodocus* I have described as the last dorsal, though there functioning as a sacral, I am as yet undecided. I believe, however, that it is, although since it is the neural spines of this and the two succeeding vertebræ that are coössified in the present sacrum, this fact might be considered by some as tending to disprove this assumption, for in *Diplodocus* it is the spines of the three median vertebræ, *the true sacrals,* that are coössified. However this may be, I am inclined to the opinion that the first vertebra which in *Diplodocus* gives support to the ilia did in fact bear what has usually been interpreted as a sacral rib and should therefore be considered as a sacral by those who accept the presence of this element as distinguishing the sacrals. The imperfect condition of all the *Diplodocus* sacra so far discovered precludes the possibility of determining this point with absolute certainty in that genus. In the type of *Diplodocus carnegii* the right side of this vertebra is present though in a somewhat imperfect condition and presents an element which, though occupying a decidedly more elevated position than that of the so-called sacral ribs in the succeeding sacrals, does however spring from the superior lateral surface of the centrum. It may therefore be considered as homologous with those elements in the true sacrals. Its position with relation to the vertebral centrum may be considered as evidence that this vertebra though functioning as a sacral is in reality a modified dorsal and that, contrary to Osborn's assertion, the sacrum in the Sauropoda may have expanded by the addition of at least one posterior dorsal.

The diapophyses of all the sacral vertebræ send downward thin vertical diapophysial laminæ. These unite at their extremity with the sacral ribs or as I prefer to call them the parapophyses[4] of their respective vertebræ to form thin partitions separating the four large sacral foramina to be seen in the inferior view of this sacrum with ilia attached, shown in Fig. 1, Plate V. Internally these foramina are enclosed by the sacral centra and externally by the extended iliac bar formed by the expanded and coalesced distal extremities of the parapophyses (sacral ribs).

The parapophyses (sacral ribs) of the first and fifth sacrals are longer but rather more slender than those of the three median or true sacrals. This is especially true of the first sacral. In this vertebra this element springs from the superoanterior surface of the centrum, continues outward for some distance as a strong bar when it expands and divides into two branches enclosing a small foramen bounded externally by the ilium and shown in Plate V., Fig. 1. The inferior of these two branches abuts against the base of the pubic peduncle, the superior unites with the diapophysial lamina in giving support to the widely expanded anterior blade of the ilium.

In the posterior sacral the parapophysis springs from the middle of the centrum at its anterior extremity and continues as a single bar, only moderately expanded distally, where it gives support to the posterior blade of the ilium. Superiorly it is united throughout its entire length with the diapophysial lamina. The diapophysis branches distally and with the posterior blade of the ilium encloses the foramen seen in Plate V., Fig. 3.

The parapophyses of the three median sacrals are all short and stout. They differ from those of the first and fifth sacrals in having their extremities expanded and coalesced so as to form a strong iliac bar not only giving support to the ilia but constituting the inner superior borders of the acetabula. These three vertebræ were the first to become coössified. Throughout the entire life of the individual they gave the chief, and during a certain period of its youth perhaps, almost the only support to the ilia. It is for these reasons that I consider these vertebræ as the only true sacrals of which the sacrum in the earliest Sauropods was alone composed.

---

[4] The homologies of these elements will be discussed more fully when we come to speak of the caudals.

Should we ever be so fortunate as to discover representatives of the very earliest Sauropod Dinosaurs it is not at all improbable that in these the sacrum will be found to consist of only these three vertebræ. This number is, however, a decided advance over that which is supposed to have constituted the sacrum in the primitive reptilia. This supposition, however, is at present purely conjectural though supported by considerable evidence. If we consider the three median vertebræ as the *true sacrals* the anterior might very appropriately be called a *dorso-sacral* and the posterior a *sacro-caudal.*

In all the functional sacrals the parapophyses spring from the anterior extremities of the centra of the several vertebræ, but in the first and second *true sacrals* there is in each instance some slight union between the posterior extremities of the centra of these vertebræ and the succeeding parapophysis as shown in Plate V., Fig. 1.

Viewed from above, the diapophyses of the sacrals in *Haplocanthosaurus* are each seen to be formed by the union of two laminæ. One of these springs from the spine of that vertebra to which the process pertains and the other from the antero-external margin of the spine of the immediately posterior sacral. These laminæ rapidly converge both inferiorly and exteriorly and unite in forming the diapophyses or transverse processes. These are on a level with the superior border of the ilium and a short distance before coming in contact with that element they expand anteroposteriorly and present broad, rugose, superior surfaces.

The neural spines of all the sacrals are extremely short as compared with the same elements in either *Diplodocus or Brontosaurus* and in this respect they more nearly resemble the same elements in *Morosaurus.* Those of the three posterior sacrals are directed upward and a little backward. The spines of the three anterior sacrals are coalesced and form an elongated bony plate. In *Diplodocus* and *Brontosaurus* it is the three (sometimes the two anterior in the former genus) true median sacrals that have the spines coalesced. Superiorly and posteriorly the spines are much expanded and they each present prominent lateral rugosities at the apex.

Seen from behind or in front the sacrum is considerably distorted by pressure. In the drawings, Plate V., this distortion has been for the most part eliminated and the sacrum appears low and very broad with the neural arches of only moderate height when compared with those of the dorsals. In so far as I have been able to determine there is in the present genus no unusual development of the neural canal in the region of the sacrum.

The principal characters of the sacrum in the present genus are well shown in Plates IV. and V., where in the former comparative views are given of the pelves of *Brontosaurus, Diplodocus* and *Haplocanthosaurus* with their respective sacra in position.

The more important dimensions of the sacrum of the type of *Haplocanthosaurus priscus* are as follows:

	mm.
Total length of the five coössified sacrals	795
Greatest expanse of transverse processes of first sacral	640
" " " " last "	700
Height of top of neural spine above bottom of centrum in first sacral	520
" " " " " " " last "	485
Anteroposterior length of three coössified neural spines	398
Height of anterior neural spine above zygapophyses	252
" posterior " " " "	180

The Caudal Vertebræ (Plate III.).—Nineteen anterior caudals were found associated with the present skeleton. Their position in the quarry relative to one another and to the sacrum are shown in Figs. 1 and 2.

The centra throughout the entire series of nineteen caudals are remarkably short when compared with the same vertebræ in *Diplodocus.* They are somewhat constricted medially and are slightly amphicœlous with the concavity of the anterior extremity more pronounced than that of the posterior. The centrum of the first caudal is the shortest of the series. From this they very gradually and slowly increase in length until the twelfth caudal is reached when they begin very gradually to decrease in length.

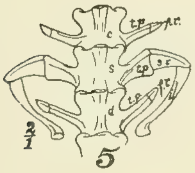
The neural spines throughout are comparatively short and directed somewhat backward. They are compressed and with rugose extremities which are quite simple throughout instead of being laterally expanded and emarginate as in caudals one to eight in *Diplodocus carnegii.*

The anterior zygapophyses are slender and extended far forward in advance of the anterior extremities of their respective centra. The posterior zygapophyses are not extended beyond the posterior extremities of the centra.

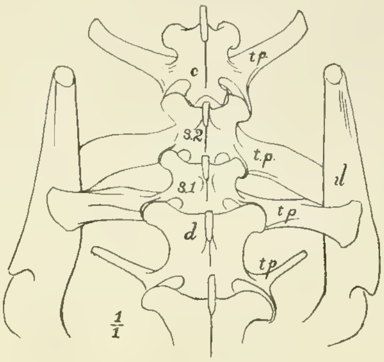
The transverse processes even in the anterior caudals are quite simple when compared with the same elements in *Diplodocus* and *Brontosaurus.* In the anterior caudals they appear as simple, broad plates of bone springing directly from the neural arches and the superior lateral surfaces of the centra. These bony plates are nearly flat and thin. They are entire instead of being perforated as in *Diplodocus,* and their posterior and anterior surfaces are entirely destitute of that series of vertical or radiating laminæ seen in the anterior caudals of *Diplodocus carnegii.* The transverse processes of the caudals decrease rapidly in size as we proceed posteriorly and in the twelfth caudal they are reduced to a rounded knob of bone on either side of the centrum near the superior border, while just above this on the middle of the side of the neural arch there is a second prominence less pronounced, however, than that on the centrum. In the thirteenth caudal the prominence on the centrum is only faintly distinguishable. In the succeeding vertebræ it has disappeared entirely, while that on the neural arch continues on the thirteenth, fourteenth and fifteenth caudals, but is wanting on the succeeding vertebræ. Of these prominences or tuberosities the superior or that one situated on the neural arch doubtless represents a rudimentary *diapophysis*, while the inferior or that situated on the side of the centrum may be considered as homologous with the *parapophysis*. It would, therefore, appear as though the transverse processes in the anterior caudals were made up of the coalesced diapophyses and parapophyses. Just what bearing this may have on the exact homologies of the so-called sacral ribs in the Sauropoda it is impossible to say. It would appear, however, that Osborn's assertion that a "sacral rib is not a transverse process"[5] is open to criticism when that term is applied to these elements in the dinosaur pelvis, or at least needs some further support, and that Marsh's statement that "each sacral vertebra supports its own sacral rib or transverse process" may not have been so far from correct as Osborn supposed it to be, though Marsh's assertion that the sacral vertebræ in the Sauropoda were without diapophyses is doubtless erroneous. If, as Osborn asserts: "The sacrum of Sauropoda (Cetiosaurs) is reinforced by the addition, not of dorsals, but of anterior caudals," it would seem quite evident that those elements which spring from the sacrals and give support to the ilia are in reality only the modified transverse processes of the caudals, and since, as has already been shown, the latter appear to have been formed by the union of parapophyses and diapophyses, there would seem very good reasons for assuming that the so-called sacral ribs which spring directly from the sacral centra are homologous with the parapophyses, while the superior bar giving support to the superior border of the ilium represents the diapophyses and that these two elements with the connecting diapophysial lamina together constitute the transverse process. According to this interpretation the so-called *sacral ribs* become morphologically quite distinct from those elements in the tailed Amphibians as described by Flower on page 66 of his "Osteology of the Mammalia," and I am inclined to the opinion that, while the articulation of the ilium with the sacrum in the Hell Bender (*Menopoma*) and other allied forms is by means of a sacral rib interposed between the ilium and the transverse process of the sacral vertebra, in the Sauropoda, as well as in all the other terrestrial vertebrates requiring more or less rigidity in this region, this interposed sacral rib, if it ever existed, has disappeared altogether, allowing the ilium to come in direct contact with the transverse processes of the sacrum. In *Menopoma* the transverse process of the sacral is stronger not only than those of the preceding and succeeding vertebræ, but it is stronger than its sacral rib, although the latter is more robust than the movable ribs borne by the transverse processes of the immediately preceding and succeeding vertebræ. It would seem more probable, therefore, that the smaller and more slender sacral rib would become obsolete than the stronger and more robust transverse process. Whether this elimination was accomplished by the complete disappearance of the sacral rib or by its fusion with the transverse process cannot be told. If by the latter process, however, the so-called sacral ribs in the Sauropod sacrum would then be homologous with the coalesced sacral ribs and transverse processes. But in the sacra of the Sauropoda and other highly specialized terrestrial vertebrates, whether reptiles or mammals, it would appear to be quite evident that in all those sacral vertebræ added to the primitive sacrum through the modification of anterior caudals it is the *transverse processes* (united diapophyses and paropophyses) that have been modified to give support to the ilia instead of true *sacral ribs* homologous with the free ribs borne at the extremities of the transverse processes in the anterior caudals of *Menopoma*, for in no instance are the transverse processes of the anterior caudals of even moderately specialized terrestrial vertebrates known to have borne such ribs. Even in the modern Iguana and in the crocodiles where the sacrum is still exceedingly primitive, consisting of only two ununited vertebræ, there are no movable or other ribs on the transverse processes of the anterior caudals and none are known to the present writer even among the earliest known Dinosauria. It does not seem at all reasonable to suppose that these ribs were present in the primitive forms in the caudal region, that they disappeared and then reappeared in the successive caudals as these were added to the primitive sacrum more especially since their presence would tend to produce instability rather than strength in that region where rigidity is especially advantageous. In Figs. 5 and 6 are given superior views of the sacra together with the immediately preceding and succeeding vertebræ in *Menopoma allegheniensis* and *Iguana tuberculata*. A study of these figures shows the marked difference in the structure of the sacrum in the two. In *Menopoma* the ilia articulate with the transverse processes of the solitary sacral through the intermedium of sacral ribs, while in the Iguana this articulation is directly with processes firmly fixed one on either side of the centra of each of the two sacrals. Whatever the exact homologies of these latter processes may be it is impossible to say with certainty, though embryology ought to offer some evidence. In general form and in position, however, it is evident that they approximate much more closely the transverse processes than true sacral ribs. If, however, they are homologous with the true sacral ribs as seen in *Menopoma*, which to the writer seems extremely improbable, it does not follow that they are "profoundly different from the dorsal ribs" as has been stated by Osborn;[5] for an examination of a skeleton of *Menopoma* will show the morphological identity of the sacral ribs with the free ribs borne at the extremities of the transverse processes alike of the anterior caudals and the entire presacral series, while the latter must be homologous with the dorsal ribs in the terrestrial vertebrates as will become apparent by a study of the skeleton of *Iguana* where the transition from the short straight ribs of the dorso-lumbar region to the elongated and curved ribs of the true dorsals is quite gradual.

---

[5] See Memoirs Am. Mus. Nat. Hist., Vol. I., Part V., p. 202.



5



6

FIG. 5. Superior view of sacral, anterior caudal and posterior dorsal or lumbar of *Menopoma alleghenienisis*, twice natural size. *s*, sacral; *c*, anterior caudal; *d*, posterior dorsal; *t.p.*, transverse process; *s.r.*, sacral rib; *il*, ilium; *f.r.*, free rib.

FIG. 6. Superior view of sacrum, anterior caudal and posterior lumbar or dorsal of *Iguana tuberculata*, natural size. *d*, posterior dorsal; *s.1*, first sacral; *s.2*, last sacral; *c*, anterior caudal; *t.p.*, transverse process except that on last dorsal which is a free rib; *il*, ilium.

In consideration of the characters just described as obtaining in the transverse processes of the caudals of *Haplocanthosaurus* in connection with those already mentioned as pertaining to the sacrum in the various genera of the Sauropoda, it appears to the present writer that the following characters relative to the structure of the Sauropod sacrum as a whole and the homologies of the different elements with those of the other vertebræ seem quite probable though not at present capable of being demonstrated with certainty.

FIRST. — *That the Sauropod sacrum is composed of five coössified vertebræ which function as sacrals.*

SECOND. — *That the three median of these five functional sacrals alone composed the sacrum in the primitive Sauropoda and may be regarded as the true sacrals.*

---

[5] Vol. I., Part V., Mem. Am. Mus. Nat. Hist., p. 201.

THIRD. — *That the number of sacrals in the Sauropoda has been increased to five by the addition of a posterior dorsal and an anterior caudal.*

FOURTH. — *That the sacrals give support to the ilia solely by means of the transverse processes (diapophyses and parapophyses).*

FIFTH. — *That there are no true sacral ribs homologous with those elements in the tailed amphibia and that the so-called sacral ribs are really homologous with the parapophyses or inferior branches of the transverse processes.*

It is true that the parapophyses (sacral ribs) of the sacrals, as also the transverse processes of the caudals in the Sauropoda are derived from centers of ossification distinct from those which give origin to the centra, and this fact may by some authorities be taken as proof that they are not portions of the transverse processes, though I should not consider it as such.

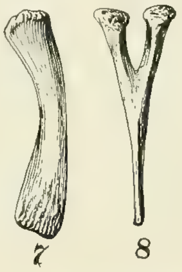
The principal dimensions sometimes materially modified by crushing of the several vertebræ in the type of *Haplocanthosaurus priscus* (No. 572) are given in the following table: In column 1 the greatest expanse of the transverse processes of the diapophyses are given; column 2, greatest length of centra; column 3, transverse diameter of centra at posterior extremity; column 4, height of neural spines

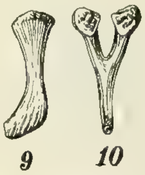
	1. mm.	1. in.	2. mm.	2. in.	3. mm.	3. in.	4. mm.	4. in.
? 14. Cervical.			259	$11\frac{3}{8}$	160	$6\frac{1}{4}$	320	$12\frac{5}{8}$
? 15. “			247	$9\frac{1}{4}$	150	$5\frac{7}{8}$	352	$13\frac{7}{8}$
1. Dorsal.	428	$16\frac{3}{8}$	224	$8\frac{3}{4}$	153	6	355	14
6. “	420	$16\frac{1}{2}$	185	$7\frac{1}{4}$	135	$5\frac{1}{4}$	568	$22\frac{5}{16}$
7. “	458	18	173	$6\frac{3}{4}$	145	$5\frac{5}{8}$	590	$23\frac{1}{4}$
8. “	457	18	165	$6\frac{1}{2}$	150	$5\frac{7}{8}$	551	$21\frac{5}{8}$
9. “	457	18	185	$7\frac{1}{4}$	154	6	583	$22\frac{7}{8}$
10. “	440	$17\frac{1}{4}$	164	$6\frac{3}{8}$	153	6	582	$22\frac{7}{8}$
11. “	430	$16\frac{7}{8}$	170	$6\frac{7}{8}$	161	$6\frac{3}{8}$	597	$23\frac{1}{2}$
12. “	425	$16\frac{3}{4}$	150	$5\frac{7}{8}$	178	7	607	$23\frac{7}{8}$
13. “	410	$16\frac{1}{8}$	146	$5\frac{3}{4}$	191	$7\frac{1}{2}$	610	24
14. “	410	$16\frac{1}{8}$	125	$4\frac{7}{8}$	203	8	615	$24\frac{1}{4}$
1. Caudal.	416	$16\frac{3}{8}$	103	4	195	$7\frac{5}{8}$	510	20
2. “	390	$15\frac{1}{4}$	82	$3\frac{1}{4}$	178	7	471	$18\frac{1}{2}$
3. “	320	$12\frac{1}{2}$	91	$3\frac{5}{8}$	190	$7\frac{1}{2}$	365	$14\frac{3}{8}$
4. “	353	$13\frac{7}{8}$	86	$3\frac{3}{8}$	165	$6\frac{1}{2}$	375	$14\frac{3}{4}$
5. “	314	$12\frac{3}{8}$	94	$3\frac{7}{8}$	175	$6\frac{7}{8}$	396	$15\frac{5}{8}$
6. “	230	$9\frac{1}{8}$	95	$3\frac{7}{8}$	137	$5\frac{3}{8}$	404	$15\frac{7}{8}$
7. “	?	?	105	$4\frac{1}{8}$	?	?	415	$16\frac{3}{8}$
8. “	216	$8\frac{1}{2}$	97	$-3\frac{7}{8}$	125	$4\frac{15}{16}$	397	$15\frac{5}{8}$
9. “			100	4	115	$4\frac{1}{2}$	?	?
10. “			114	$4\frac{1}{2}$	165	$6\frac{1}{2}$	345	$13\frac{1}{2}$
11. “			105	$4\frac{1}{8}$	105	$4\frac{1}{8}$	338	$13\frac{1}{4}$
12. “			110	$4\frac{3}{8}$	110	$4\frac{3}{8}$	314	$12\frac{3}{8}$
13. “			101	4	114	$4\frac{1}{2}$	298	$11\frac{3}{4}$
14. “			100	-4	109	$4\frac{1}{4}$	261	$10\frac{1}{4}$
15. “			100	$3\frac{7}{8}$	107	$4\frac{1}{4}$	268	$10\frac{1}{2}$
16. “			99	4	101	4	261	$10\frac{1}{4}$
17. “			95	$3\frac{3}{4}$	100	$+3\frac{7}{8}$	237	$9\frac{3}{8}$
18. “			92	$3\frac{5}{8}$	100	-4	229	9
19. “			91	$3\frac{5}{8}$	92	$3\frac{5}{8}$	210	$8\frac{1}{4}$

above middle of inferior border of centra in presacrals and above inferior border of posterior end in postsacrals.

The inconsistencies that appear in the above table of measurements are due to the varying amount of crushing to which the different vertebræ were subjected while entombed in the sandstones. In this connection it should be remembered that these animals lived in a period long previous to that which witnessed the final upheaval of the front range of the Rocky Mountains and that the bones, as well as the sandstones in which they were imbedded, have been subjected to the enormous pressure which effected the upheaval of that mountain range. Little wonder that they are in many instances much crushed and distorted. It thus happens that the measurements given above are of value only as giving a general idea as to the several dimensions of the various vertebræ. In most instances they cannot be considered as representative of the exact measurements and therefore capable of being compared critically with those of other skeletons.

The Chevrons (Figs. 7, 8, 9, 10). — Only two chevrons were found. One of these (Figs. 7 and 8) was found in position between the eighth and ninth caudals. It does not differ materially from the chevron of the same region in *Diplodocus* or *Brontosaurus.* It is Y-shaped with the open portion somewhat abbreviated and the inferior portion elongated, compressed and with spatulate extremity. The articular surfaces of opposite sides at the proximal ends are not confluent. The length of this chevron is 313 mm. When seen from the side, it curves less strongly backward at the distal end than does the same chevron in *Diplodocus.*





FIGS. 7 and 8, chevron between caudals 8 and 9, side and posterior views respectively, one-tenth natural size.

FIGS. 9 and 10, chevron between caudals 13 and 14, side and posterior views respectively, one-tenth natural size.

The other chevron (Figs. 9 and 10) was found in position articulating with caudals thirteen and fourteen. It differs from the one just described in its smaller size and in the more elongated open portion of the Y as compared with the closed inferior portion. At the point where the two branches meet it is greatly constricted antero-posteriorly, while distally it is much expanded in the same direction, but without the anterior and posterior projections which are already quite prominent in the same and the preceding chevron in *Diplodocus.* This chevron has a length of 184 mm.

The Ribs (Figs. 11, 12 and 13). — The ribs do not differ essentially from those of other members of the Sauropoda. They increase in length and strength quite rapidly from the first to the fourth when they continue subequal in length until in about the region of the ninth or tenth. Posterior to these, they rapidly become shorter and more slender. The ribs of the anterior and mid-dorsal region are much expanded proximally where they present a rather deep concavity on the posterior surface, while the anterior surface in the same region is convex. Beyond this they become subcircular in cross-section and somewhat spatulate at their distal extremiies. The ribs of the posterior region are decidedly less expanded proximally and in the middle they are semicircular in cross-section.

Figs. 11, 12 and 13 represent respectively anterior views of the supposed second, fourth and thirteenth ribs. The second rib has a length of 911 mm., the fourth 1,394 mm. and the thirteenth 710 mm. Compared with the size of the animal as a whole the ribs of *Haplocanthosaurus* are neither long nor robust. Throughout the entire series the capitulum and tuberculum are well separated. The capitulum is pediceled while the tuberculum is sessile, save in the anterior ribs where it is also pediceled.

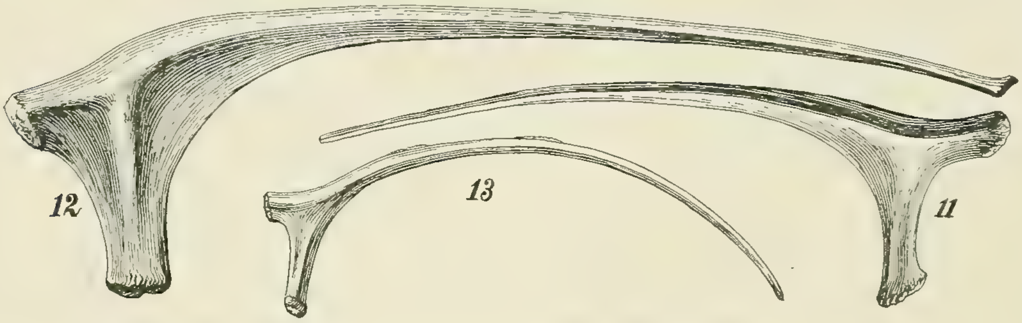


FIG. 11. Anterior view of second? rib of right side, one-tenth nat. size.
FIG. 12. Anterior view of fourth? rib of left side, one-tenth nat. size.
FIG. 13. Anterior view of thirteenth? rib of left side, one-tenth nat. size.

The Pelvis (Plates IV. and V.).

All the elements of the pelvis were found approximately in position and in a splendid state of preservation.

The Ilium (Plate IV., Fig. 3). — In general form the ilium resembles that of other members of the Sauropoda. In the present skeleton both ilia were found attached to the sacrum which lay imbedded in the sandstones with the spines directed upwards but reclining a little on its right side. It thus happened that these elements received the pressure of the superincumbent rocks in a direction obliquely vertical and from the left. This pressure was sufficient to accomplish considerable crushing and the superior borders of the ilia have been considerably flattened and instead of describing the arc of a circle as was doubtless the case before this distortion took place, for a considerable distance along their superior borders they now present a nearly flat surface. In the drawings this distortion has not been entirely eliminated.

The ischiac peduncle is broad and sessile with the transverse diameter of the articular surface for the ischium considerably exceeding the anteroposterior diameter.

The pubic peduncle is elongate, extending far below the inferior border of the ilium. It forms most of the anterior border of the acetabulum. The articular surface for the pubis has the transverse diameter greater than the anteroposterior. At its base the pubic peduncle is supported internally by the parapophyses of the dorso-sacral and the first true sacral vertebra as shown in Plate V., Fig. 11.

The ilium is produced far in front of the pubic peduncle into a broad anterior blade. At its extremity this anterior blade of the ilium is broad instead of pointed as in *Diplodocus* and *Brontosaurus.* In superficial area the anterior blade of the ilium constitutes nearly one half of that element. Internally it is supported by the powerful and widely expanded diapophysis of the dorso-sacral.

The ilia are not produced far behind the ischiac peduncles and the posterior blades are therefore short but rather broad.

The upper one-half of the acetabular border is formed by the ilium, the pubic and ischiac peduncles and the acetabular bar formed by the united extremities of the parapophyses of the three true sacrals.

The anterior extremities of the ilia of opposite sides are very widely separated and the posterior extremities less decidedly so while in the middle, both superiorly and inferiorly the ilia of opposite sides approach more nearly to each other. It thus happens that the diapophyses and parapophyses of the three true sacrals are shorter than those of the dorso-sacral and sacro-caudal.

The Pubis (Plate IV., Fig. 3, and Plate V., Fig. 2).—The pubis is proportionately short and stout and greatly expanded proximally. At their distal extremities the internal borders of the pubes were in contact for a short distance only. Above this point of contact, when in position, the pubes were separated by an elongated aperture 300 millimeters in length, while above this aperture they meet again and form an elongated pubic symphysis about 300 millimeters in length. In either instance the union between the pubes of opposite sides was ligamentary. The direction and position of the superior of the two pubic symphysial surfaces is horizontal and ventral rather than vertical. The pubis forms the antero-inferior one fourth of the acetabulum. The pubic foramen is very large and somewhat elliptical in outline; just posterior to and above it there is an extended sutural surface for contact with the ischium.

The Ischium (Plate IV., Fig. 3, and Plate V., Fig. 3).—As compared with the pubes the ischia were slender. Proximally they expand and form the postero-inferior one fourth of the acetabular border. Beneath the acetabular border they present broad, rugose, sutural surfaces for articulation with the pubes. Posteriorly the ischia contract rapidly and form broad flat bars with broadly rounded external surfaces. These bars converge and meet distally where they are coössified to form a symphysis about 195 millimeters in length.

The form and principal characters of the different elements of the pelvis are well shown in the figures in the plates accompanying this memoir.

The principal measurements of the different elements of the pelvis are as follows:

	mm.
Greatest length of ilium	827
Distance from inferior extremity of pubic peduncle to top of iliac crest	512
“ “ “ “ ischiac “ “ “ “	332
Length of pubic peduncle below superior border of acetabulum	249
Expanse of ilia at anterior extremity	1140
“ “ “ “ posterior “	810
“ “ pubic peduncles	786
“ “ ischiac “	685
Length of pubis	693
Greatest breadth of pubis	432
Least “ “ “	165
Length of ischia from middle of acetabular border to distal end	790
Extent of acetabular border of ischium	210
Breadth of ischium just above symphysis	85
Depth “ “ “ “ “	50

The Femur (Fig. 14).

Unfortunately the femur is the only element preserved of either the fore or hind limbs and this is not entirely complete, though sufficiently well preserved to show most of the more important characters. As shown in the diagram it was found not far removed from its normal position relative to the pelvis, so that there can be no reasonable doubt that it pertains to the same skeleton. It does not differ materially from the femur in other members of the Sauropoda although as compared with the other portions of the skeleton it appears rather long and stout. There is a low and elongated fourth trochanter on the postero-internal margin midway between the proximal and distal extremities, and just external to this is a shallow concavity with a markedly rugose surface. The external condyle is larger than the internal and they are well separated by a deep intercondylar notch. The head is large and hemispherical in form but without distinct neck. The articular surface is very rugose and this rugosity is continued along the superior surface of the *greater trochanter* to the external surface of the shaft. Both the internal and external margins of the shaft of the femur curve very gently outward as shown in Fig. 14. The principal dimensions of the femur are as follows:

	mm.
Length	1275
Transverse diameter at proximal end	353
" " " distal "	309
" " " middle of shaft	207

CONCLUSIONS.

When considered together the remains upon which the present genus and species are based indicate an animal of rather unusual proportions for a member of the Sauropoda. The number of dorsals and the comparative length of the individual dorsals indicate a thoracic region proportionally longer than in *Diplodocus*, *Brontosaurus* or *Morosaurus*. While the cervical region appears somewhat abbreviated and the caudal region must have been remarkably short as is indicated by the reduced length of the individual vertebræ, though this was probably made less apparent by an increase in the number of caudals. Judging from the femur alone the limbs were comparatively long, and the animal proportionately high and short for a Sauropod dinosaur.

HAPLOCANTHOSAURUS UTTERBACKI sp. nov.
(No. 879.)

The present species is named for Mr. W. H. Utterback, its discoverer, and in recognition of his services to vertebrate paleontology.

Char. Sp.: It is readily distinguished from *H. priscus*, the type species of the genus by the character of the posterior dorsal centra which are rather more opisthocœlous than in the type species. The fully adult indiviual was doubtless of larger size in the present than in the first named species of the genus. But the most distinctive character is to be found in the sacrum which, in the present species, has the five neural spines normally coössified. The first four are coössified throughout their

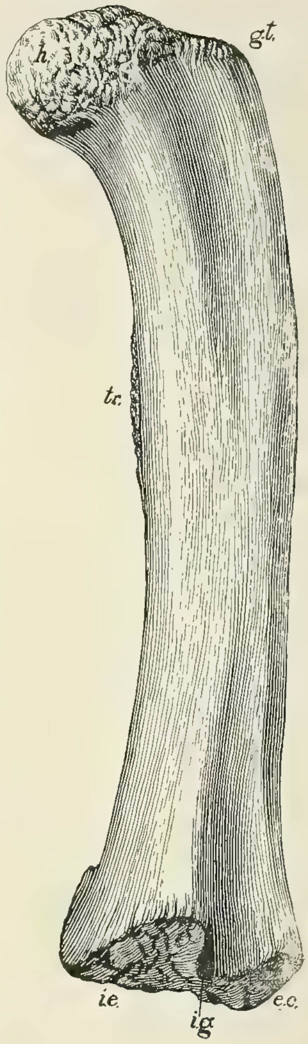


FIG. 14. Left femur of *Haplocanthosaurus priscus*, front view, seen obliquely from within (No. 572), $\frac{1}{10}$ natural size. *h.*, head; *gt.*, greater trochanter; *tr.*, fourth trochanter; *i. e.*, internal condyle; *e.c.*, external condyle; *i.g.*, inter-condylar groove.

entire length, forming a long bony plate. The union between the fourth and fifth is limited to the extremities while medially they are separated by an elongated foramen. In *H. priscus* only the spines of the three anterior sacrals are coössified, those of the first and second sacrals remaining free. This difference exists notwithstanding that the type of the present species was scarcely adult, the sacral centra neither being coössified with one another nor with their neural arches. By some this character might be considered as of generic importance although I prefer to consider it as of only specific value since in all other parts of the skeleton preserved there are no distinguishing characters which could be considered as of generic value.

Description of the Type. (No. 879.)

The type of the present species consists of a left scapula and right coracoid, several ribs and thirty-five more or less complete vertebræ distributed as follows: Ten cervicals, thirteen dorsals, five sacrals and seven caudals. For the most part these vertebræ are complete, but in a few instances they are represented only by isolated spines and neural arches without centra, or by centra without spines and neural arches, and one anterior cervical, probably the axis or the succeeding cervical, is represented only by a portion of the neural arch. The position of these bones relative to one another as they were found in the quarry is shown within the dotted line in the upper left-hand corner of the diagram shown in Fig. 1 where the positions of the different bones are indicated as follows:

1 = cervical 3, placing the number of cervicals at fifteen.
2 = “ 4.
3 = “ 8.
4 = “ 9.
5 = “ 10.
6 and 6′ = “ 11.
7 = “ 12.
8 = “ 13.
9 = “ 14.
10 = “ 15, or last of cervical series.
11 and 11′ = dorsal 2.
12 = “ 3.
13 and 13′ = “ 4.
14 and 14′ = “ 5.
15 and 15′ = “ 6.
16 = “ 7.

17 = dorsal 8.
18 = “ 9.
19 = “ 10.
20 = “ 11.
21 = “ 12.
22 = “ 13.
23 = “ 14.

Sa = spines and transverse processes of sacrals; *a*, *b*, *c*, *d*, *e* represent respectively the spines of sacrals 1, 2, 3, 4, and 5.

24 = centrum of sacral 4.
25 = “ “ “ 5.
27 = caudal 1.
28 = “ 2.
29 = “ 3.
30 = “ 4.
31 = “ 5.
32 = “ 6.
33 = “ 7.
34 = parapophysis (sacral rib) of first sacral.
35–39 inclusive are ribs.
S = left scapula.
c = right coracoid.

Shaded bones in diagram do not pertain to *Haplocanthosaurus*.

As will appear by a critical examination of the diagram the vertebræ of the cervical and anterior dorsal regions were much scattered and displaced before finally becoming imbedded in the sands which later become solidified into the sandstones of almost granitic hardness in which they were found encased. In the following description of the vertebral column the reader should bear in mind that save for the third dorsal and the first and second caudals the centra were detached from the neural arches. Owing to the age of the individual there was as yet only a sutural union between the centra and the neural arches of the respective vertebræ. In most instances the centra, while not directly attached to their respective arches, were either found in position or only slightly removed from their normal positions relative to one another. In some instances, however, as with dorsals 2, 5 and 6, the centra and neural arches were found separated by a distance of from two to four feet, while a few vertebræ are represented by their centra or neural arches only.

The Cervicals. Plate II., Series 3 and 4.

The Third (?) Cervical (Plate II., Fig. 3, Series 4). — The most anterior vertebra of the cervical series pertaining to this skeleton I have referred to the third although it may pertain to the axis. Its fragmentary condition precludes the possibility of determining the exact position with certainty. Its position in the quarry is shown at 1 in the first diagram. It consists of the posterior portion of the neural arch with the posterior zygapophyses and it could hardly have occupied a position posterior to the third cervical although it may pertain to the axis.

The Fourth Cervical (Plate II., Fig. 4, Series 4). — A little to the right of the cervical fragment just described the present vertebra, which I interpret as the fourth cervical, was found. Its exact position in the quarry is shown at 2 on the diagram. It is essentially complete and but little distorted, though as with all the cervicals of this series the rib is disarticulated as was to be expected considering the age of the individual. The posterior zygapophyses and transverse processes are widely expanded. Near the anterior extremity and on either side of the centrum a strong process springs from the inferior lateral border. At the extremity this expands into a capitular facet for the articulation of the capitulum of the cervical rib. These processes as well as the similar, though less pronounced ones found on the succeeding cervicals may possibly be homologous with the parapophyses. In the present vertebra they are produced far below the inferior border of the centrum. The pleurocentral cavity is deep and invades the base of the ball. It is confluent with a rather deep cavity found on the superior surface of the process which supports the capitular rib facet. It is imperfectly divided into anterior and posterior cavities by a low rounded ridge which may be regarded as an incipient oblique lamina. The centrum is markedly opisthocœlous with the cavity of the posterior extremity subcircular in outline. The inferior surface of the centrum is broad and there are five shallow infracentral cavities. One of these, the posterior, is medial, and the anterior four are lateral, arranged two on either side of the central line, one at the base of and two posterior to the processes which support the rib facets. The centrum is much contracted medially.

The Eighth Cervical (Plate II., Fig. 8, Series 4). — Between the vertebra just described and the next in our series it is evident that a number are missing. I have estimated the number of missing vertebræ at three. This would make the position of this vertebra the eighth in the series, a position with which it agrees very well if we commence with the last of the series and work forward, so that I have but little doubt that this was its correct position. It is essentially complete and not badly crushed or distorted. Save for its greater size in its general form it very closely resembles the vertebra just described. The pleurocentral cavities however are more completely divided into anterior and posterior moieties by the presence of more pronounced oblique laminæ. There is a single large infracentral cavity and the cup is broader than deep. The anterior zygapophyses are supported inferiorly by short and rather slender inferior branches of the prezygapophysial laminæ while inferior branches of the diapophysial laminæ give support to the broad diapophyses which bear at their extremities the tubercular rib facets. The position of this vertebra in the quarry is shown at 3 in the diagram.

The Ninth Cervical (Plate II., Fig. 9, Series 4). — This vertebra found at 4 in the diagram of the quarry was not far removed from the preceding. It consists of the centrum with the posterior and anterior zygapophyses still in position. It is much crushed and distorted but in so far as it is possible to determine, it agrees fairly well with what we should expect to find in the ninth cervical. It has been erroneously drawn as complete in Plate II., Fig. 9.

The Tenth, Eleventh, Twelfth and Thirteenth Cervicals (Plate II., Figs. 10, 11, 12, 13, Series 3). — These four vertebræ are in each instance well-nigh perfect and they display such a gradation of progressive characters that there can be no doubt as to their constituting a continuous series.

The neural spines and posterior zygapophyses become successively more elevated as we proceed backward in the series. The spines however show no tendency to divide, there being scarcely an emargination at the summit even in the last of the four. The posterior zygapophyses become successively more expanded and the suprapostzygapophysial cavities become deeper and broader. The position of these vertebræ in the quarry was as follows: The tenth was found at 5, the neural arch and spine of the eleventh was found at 6, and the centrum at 6′, the twelfth is shown at 7 and the thirteenth at 8.

The Fourteenth Cervical (Plate II., Fig. 14, Series 3). — Only the centrum of this vertebra was recovered; it was found at 9 on the diagram. It is considerably crushed, especially anteriorly but there is no doubt that it was a cervical and that its position was posterior to the thirteenth. Its size, length and general characters indicate that it belonged immediately behind the thirteenth I have, therefore, regarded it as the fourteenth.

The Fifteenth Cervical (Plate II., Fig. 15, Series 3). — This is represented by a well-preserved neural arch and spine without centrum found at 10 as shown on the diagram. The difference between this spine and that of the thirteenth is such as to preclude the possibility of its pertaining to the fourteenth or immediately succeeding cervical. I have, therefore, assigned it to the fifteenth or last cervical, with which it agrees very well when compared with the spine of that vertebra in *H. priscus* where there can be no question as to the proper position relative to the dorsals. Moreover if the spine of the fourteenth cervical in *H. priscus* be interposed between the present spine and that of the thirteenth cervical in the present skeleton they are seen to form a well-graduated series leaving little doubt that the positions assigned to the various vertebræ of this region of the cervical series in the skeleton under consideration are correct. The neural spine is faintly emarginate at the apex. The depth of the emargination is 4 mm.

The Dorsals. (Plate II., Series 1 and 2.)

The Second Dorsal (Plate II., Fig. 2, series 2.) There is in the vertebral series of the present skeleton no vertebra corresponding to the first dorsal in *H. priscus.* That vertebra is apparently unrepresented in the present series. The neural arch and spine found at 11′ fits fairly well on the centrum found at 11 and I have considered them as pertaining to the second dorsal. As to the neural spine and arch there can be little doubt as to this determination, but as to the position of the centrum, it is by no means certain that it does not pertain to the first rather than the second dorsal. Indeed as regards the length and form of the centrum, character of the pleurocentral cavities, and position of the capitular rib facet, it would appear to more properly pertain to the first dorsal than to the second, while the widely separated position (about four feet) in which they (the centra and neural arch) were found might be taken as an indication that they pertain to different vertebræ. I have associated this centrum and spine in the same vertebra for no other reason than that when adjusted to one another they seem to agree fairly well. I believe it quite possible, even probable, that the centrum pertains to the first dorsal. As regards the neural arch and spine however, after comparing them with those of the first dorsal in *H. priscus,* there can be no reasonable doubt but that they pertain to the second dorsal. This position is indicated by the character of the anterior branch of the horizontal lamina which is much less modified to give support to the scapula than in the first dorsal of *H. priscus.* The articular surfaces of the postzygapophyses have assumed a more perpendicular position in anticipation of the hyposphene-hypantrum method of articulation that obtains in the median and posterior dorsals. The neural spine is passing from the widely expanded scoop-like element seen in the posterior cervicals and dorsal one to the simpler form characteristic of the median and posterior dorsals. The superior branches of the postzygapophysial lamina continue, however, confluent with the neural spine, extending to its very apex and enclosing laterally a rather deep cavity which, nevertheless, is much less deep than in the last cervical of this series or the first dorsal of *H. priscus*. As in the succeeding dorsals the distance between the anterior and posterior zygapophyses is much abbreviated. There is a very faint emargination at the apex of the neural spine with a depth of only 7 mm.

The Third Dorsal (Plate II., Fig. 3, Series 2).—This vertebra lay on end as shown at 12 in the first diagram. Owing to the position in which it lay in the quarry its centrum was much shortened by the pressure to which it was subjected, the ball having been forced down into the pleuro-central cavities and the whole centrum telescoped as it were. Fortunately the neural arch and spine are in a splendid state of preservation. They are still held in position with the centrum, though the sutures are very distinct. The spine when compared with that of the preceding vertebra is much modified in the direction of the conditions that obtain in the succeeding dorsals. It has assumed a nearly vertical position instead of being inclined forward as in the preceding dorsals and cervicals.

It is very much compressed antero-posteriorly and is still connected with the posterior zygapophyses by the superior branches of the post-zygapophysial laminæ. In the present vertebra however this lamina does not run obliquely upward and backward in a direct and straight line from the zygapophysis to the top of the neural spine as in the preceding dorsals and the cervicals, but it extends backward, rising but little until it reaches the vertical plane of the anterior surface of the spine when it rises vertically as a thin narrow lamina ascending to the apex of the spine. The degree of differentiation in the neural spines of this and the immediately preceding vertebra is the most marked of any of the vertebræ even in this region where the characters of the different vertebræ are seen to change so rapidly. The apex of this spine is also faintly emarginate, the notch having a depth of 9 mm. The position of the capitular rib facet is at the supero-anterior angle of the pleurocentral cavity.

The Fourth Dorsal (Plate II., Fig. 4, Series 2).—The centrum and spine of this vertebra lay as shown at 13 and 13′ in the diagram. They are both well preserved, and the nature of the spine and transverse processes demonstrate beyond a reasonable doubt that its position in the vertebral column was immediately posterior to the vertebra just described. The spine is now quite perpendicular and more elevated. It is much compressed antero-posteriorly but somewhat expanded transversely. Its anterior surface is transversely convex, the posterior is concave, forming a long, shallow trough or scoop not nearly so deep as in the preceding vertebræ. The transverse processes in this and the immediately preceding vertebra are assuming a more elevated position, the neural arches are becoming higher and the transverse processes instead of being horizontal are directed successively more and more obliquely upward as in the succeeding dorsals.

The Fifth, Sixth, Seventh, Eighth, Ninth, Tenth and Eleventh Dorsals (Plate II., Figs. 5–11, Series 1 and 2). — The neural arches and spines of all these vertebræ were found interlocked by their zygapophyses as shown in the diagram from 14–20 inclusive. The centra of the fifth and sixth had become detached and lay as shown at 14′ and 15′. The remaining centra were in position at the base of their respective spines. The neural spines, transverse processes, capitular rib facets, neural arches, etc., form a regularly graudated series except that the capitular rib facet of the sixth is much larger than in the other vertebræ. The neural arch, spine and transverse processes of the fifth were much injured, but the spine is nearly entire and it is evident that it pertained to the vertebra immediately posterior to that just described as indicated also by the centrum. The spine is still compressed anteroposteriorly but decidedly deeper in that direction than the spine of the vertebra just described. In the spine of the succeeding or sixth dorsal the transverse and anteroposterior diameters are subequal. A hyposphene-hypantrum articulation begins with the sixth dorsal and continues throughout the remaining dorsal series.

The Twelfth, Thirteenth, and Fourteenth Dorsals (Plate II., Figs. 12–14, Series 1). — These vertebræ do not differ materially from the same vertebræ already described as pertaining to the type of *H. priscus.* They were found as shown at 21, 22 and 23 in the diagram, interposed between the series just described and the anterior extremity of the sacrum. As shown in the diagram the neural arches were in position relative to one another but the centra were a little removed from their normal positions. They are all in a nearly perfect condition.

If the reader has followed carefully the above description of the dorsals pertaining to the present skeleton together with those which pertained to the type of *H. priscus* and will examine the accompanying figures it will have become apparent that the complete dorsal series in *Haplocanthosaurus* must have consisted of not less than fourteen free vertebræ while it is scarcely possible that there were more than fourteen. This is a very marked increase over the number (ten) which is believed to have formed the complement of free dorsals in *Diplodocus, Brontosaurus and Morosaurus.* Nor does this increase in the number of dorsals in the present genus seem to have been made at the expense of the cervical series, for as near as we can judge, *Haplocanthosaurus,* like *Diplodocus,* was provided with fifteen cervicals. Our determination of the number of cervicals however does not rest on anything like so good a basis as does our determination of the number of dorsals but there can be little doubt but that the number of presacrals in the present genus exceeded that of the same series in *Diplodocus*.

The Sacrals. (Figs. 15, 16 and 20.)

The sacrum of the present skeleton differs considerably from that of the type of *H. priscus*. Its position in the quarry is shown in the diagram at *Sa*. Only the neural spines and diapophyses, the parapophyses of the right side and the centra of the fourth and fifth sacrals are preserved. The neural spines of the first, second, third and fourth sacrals are confluent and firmly coössified throughout their entire length, while the spine of the fifth is coössified only at the top and the bottom with that of the fourth sacral, and medially there is an elongated foramen between these spines shown at *f* in fig. 15. The spines of the two anterior sacrals rise nearly perpendicular, those of the third and fourth are directed somewhat backward, while that of the fifth is again directed forward to meet at the apex that of the fourth sacral. The spines of the first, second, third and fourth sacrals bear diapophysial laminæ, and at the summit these expand into prominent rugosities.

The diapophyses of the first and second sacrals are directed outward, forward and a little upward, nearly parallel to one another. Those of the succeeding sacrals are directed outward, backward and a little upward, parallel to one another, but that of the third meets that of the second in an acute angle at the base of the diapophysial lamina, forming a letter V with the apex directed toward the spine. The diapophysis of the third sacral is formed by the union of branches from the diapophysial laminæ of the second and third sacral spines.

All the parapophyses (sacral ribs) of the right side are present and nearly complete. They all show sutural surfaces for articulation with the sacral centra and with the ilium. The parapophyses are shown in position in the view of the sacrum from the right side seen in Fig. 15, while comparative front views of the individual parapophyses are given in Fig. 16, *a*, *b*, *c*, *d*, *e*, which represents the series from the first to the fifth, respectively. Of the five parapophyses the first is the more slender. It is triangular in outline, with an emarginate base describing a nearly complete semicircle. It may be described as composed of a horizontal and ascending branch. The surface for contact with the centrum is not greatly expanded. There are two surfaces for contact with the ilium, one inferior, the other superior and separated by a distance of about 215 mm. The inferior of these surfaces is more pronounced and both show prominent rugosities. The anterior surface of this bone is convex, the posterior concave. Between the inferior and superior surfaces for contact with the ilium there was an elongated foramen enclosed externally by the ilium and internally by the ascending branch.

In the parapophysis of the second sacral the horizontal branch has become very strong and much expanded at either extremity for contact with the centrum and ilium. The ascending branch is broad but very thin, and presents at its extremity only a small rugosity for contact with the ilium. The foramen between it and the ilium was broader than that separating the same branch of the preceding parapophysis. Immediately above the surface for contact with the centrum there is a rugosity which doubtless gave support to the descending branch of the diapophysis, but it would appear that the diapophysis and parapophysis were not in contact throughout their entire length, but were separated for a considerable distance by an elongated foramen. The external extremity of the horizontal branch is greatly expanded transversely so as to unite with the same element in the succeeding parapophysis, to form the acetabular bar and give additional support to the ilium.

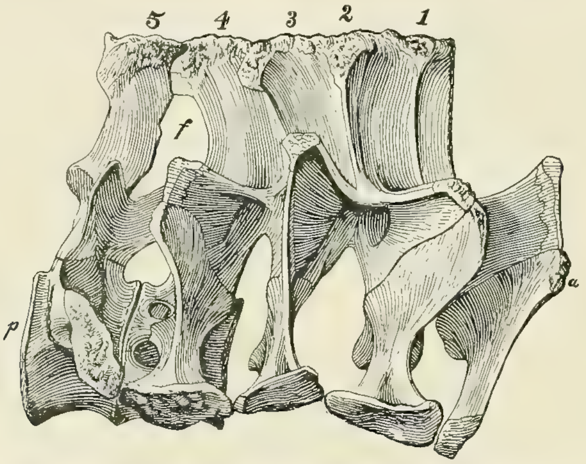


FIG. 15. Sacrum of *Haplocanthosaurus utterbacki*, seen from right side, $\frac{1}{10}$ natural size. *a*, anterior extremity; *p*, posterior extremity; *1*, *2*, *3*, *4*, *5*, spines of first to fifth sacrals; *f*, foramen between spines of fourth and fifth sacrals.

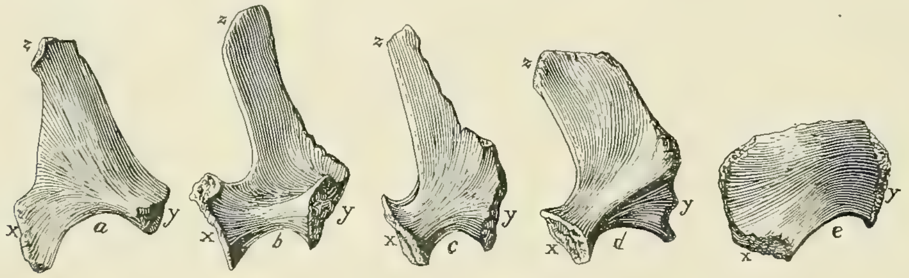


FIG. 16. Anterior view of disarticulated parapophyses (sacral ribs) of *Haplocanthosaurus utterbacki*, $\frac{1}{10}$ natural size. *a* to *e*, first to fifth respectively; *y*, surface for contact with sacral centrum; *x*, inferior surface for contact with ilium; *z*, superior surface for contact with ilium.

The parapophysis of the third sacral differs from that just described in its shorter horizontal branch and narrower and more slender ascending branch. The shortening of the horizontal branch is of course brought about by the inward curvature of the ilium in the region of the acetabulum.

The fourth parapophysis differs from all the preceding in its widely expanded ascending branch which curves very gently backward. The horizontal branch is stout and longer than that of the third parapophysis.

The fifth and last parapophysis differs from all the preceding in the absence of any ascending branch. The horizontal branch is greatly expanded vertically, and the articular surface for the ilium is elongate so as to give support to the ischiac peduncle and posterior blade of the ilium. The principal characters of the parapophyses are well shown in the accompanying figures.

Only the centra of the fourth and fifth sacrals are preserved. Fortunately these are well preserved. The parapophyses of the right side fit very well when adjusted to their respective vertebræ. Neither of these vertebræ show any marked enlargement of the neural canal. They are both constricted medially, and the distal extremity of the fifth is considerably expanded for contact with the first caudal. The centrum of the fifth sacral is decidedly heavier than that of the fourth.

The principal measurements of the different sacral elements in the type of the present species are as follows:

	mm.
Distance along crest of the five coössified sacral spines	460
“ “ “ “ four anterior “ “	375
“ from anterior zygapophyses of first sacral to posterior zygapophyses of fifth sacral	575
Expanse of diapophysis of third sacral	375
Greatest length of horizontal branch of first parapophysis	213
“ height of ascending “ “ “ “	300
“ length of horizontal “ “ second “	146
“ height of ascending “ “ “ “	300
“ length of horizontal “ “ third “	128
“ height of ascending “ “ “ “	277
“ length of horizontal “ “ fourth “	150
“ height of ascending “ “ “ “	250
“ length of horizontal “ “ fifth “	225
Length of fourth sacral centrum	132
Depth “ “ “ “ at posterior end	166
Width “ “ “ “ “ “ “	132
Length “ fifth “ “ “ “ “	120
Depth “ “ “ “ “ “ “	182
Width “ “ “ “ “ “ “	181

The Caudals. (Plate II., Series 5.)

Only the seven anterior caudals are preserved in the type of the present species and these differ very little from the same vertebræ in *H. priscus*, except that the transverse processes are less well developed and not so much expanded supero-inferiorly. Owing to the age of the individual the neural arches and transverse processes are not coössified with their respective centra although those of the first two are still held in place. The neural spines are short and stout and very rugose. That of the first is curved rather strongly backward. All the centra are very short and biconcave. The anterior zygapophyses are acutely wedge-shaped and extend well forward with the articular surfaces facing decidedly more inward than upward. The posterior zygapophyses are only flattened surfaces at the bases of the neural spines. The transverse processes are suturally connected both with the centra and the neural arches.

The Vertebral Formula.

From the foregoing descriptions of those portions of the vertebral column preserved in the type of the present species and in that of *H. priscus* it will have become apparent that we must await future discoveries to determine with accuracy the vertebral formula of *Haplocanthosaurus.* The number of sacrals however may be considered as being definitely fixed at five, while the number of dorsals could not have been less than fourteen, thirteen of which are represented in the skeleton constituting the type of *H. utterbacki.* In this skeleton it would appear that only the first dorsal is missing, and fortunately that vertebra in the type of *H. priscus* was found interlocked by its zygapophyses with the last cervical. Although the various vertebræ in the anterior dorsal region of the type of *H. utterbacki* were for the most part found in such a scattered and disarticulated condition as to afford little direct evidence concerning the exact positions relative to one another which they occupied in the skeleton during the life of the animal, yet a close examination and careful study of the vertebræ has convinced me that there are no duplicates among the thirteen dorsals described and that there can be no question but that all of the thirteen are dorsals and that they pertained to the skeleton of one and the same individual. That the first dorsal is wanting in this skeleton is shown by a careful comparison of the neural arch and spine of the most anterior of this series with that of the known first dorsal in *H. priscus*, from which, as has been shown in the descriptions, it differs materially and in the direction of those characters which we should expect in the succeeding or second dorsal. For these reasons I have referred this spine to the second dorsal although the centrum which was found detached and separated, but which in the description and figure I have associated with this spine may, as I have already remarked, pertain to the first dorsal. I do not think it at all probable that more than one dorsal is missing from the series in *H. utterbacki* and it is with a feeling of considerable confidence that I place the number of dorsals in this species at least, at fourteen. Fully realizing the character of the evidences upon which I have arrived at this conclusion I have spared no pains to present to the student all the evidence furnished by the material at my command, both as regards its anatomical characters and the position in which the different bones were found in the quarry. Aided by the accompanying diagrams and with the type material at his disposal the future student will be in full possession of all the evidence in the case and will therefore be in a position to decide for himself as to the worth of my conclusions.

In placing the number of free dorsals at fourteen I am fully aware that this is a considerable advance over the number that has of late come very generally to be considered as characteristic of other members of the Sauropoda (*Diplodocus, Brontosaurus, Morosaurus*). Considering however the less specialized nature of the present genus and the great differences seen, in other important characters, when compared with the genera just mentioned I do not consider this increase in the number of dorsals as at all remarkable, for it is not at all impossible that the earlier ancestors of *Diplodocus, Brontosaurus and Morosaurus* were provided with an equal number of free dorsals and that the reduction to ten in each of those genera may be regarded as a specialized character attendant upon and which took place along with that remarkable specialization which, as is well known, they must have undergone in other respects and which is most marked in that exceedingly complicated arrangement of laminæ and buttresses seen in the dorsal and cervical vertebræ of those genera.

It will doubtless have been remarked that in describing the cervicals I have placed the number of vertebræ of this region at fifteen, the number present in *Diplodocus.* It must be admitted, however, that the material at hand does not afford a very reliable basis for determining the number of cervicals and I should not be at all surprised if the actual number of cervicals in *Haplocanthosaurus* should prove to be one or two less than in *Diplodocus.* In placing the number at fifteen, as in the latter genus, I assume that *Haplocanthosaurus* was provided with four more presacrals than was *Diplodocus.* While my estimate of the number of cervicals in the present genus may prove to be too great, it is hardly possible that it will be reduced by more than two. This would still give to *Haplocanthosaurus* two more presacrals than are present in *Diplodocus.* It would thus appear that in the various genera of the Sauropoda the number of presacrals differed and that the number of cervicals is not entirely dependent upon an increase or decrease in the number of dorsals in any genus within the group. Still it is easily conceivable that in any genus or species the presacral formula might vary, without increasing the total number of presacrals in the individual, according as the exact position in the presacral series at which the change from cervicals to dorsals took place, and I am inclined to the opinion that as a rule in any given genus of the Sauropoda where marked specialization has taken place, there has been a tendency to increase the number of cervicals at the expense of the dorsal series, due to the gradual shifting of the pectoral girdle from a more advanced to a more posterior position, by which process anterior dorsals have been transformed into posterior cervicals and the cervical region considerably elongated at the expense of the dorsal. An extreme instance of this is to be seen in *Diplodocus carnegii* where the disparity in length in the neck and dorsum, probably due primarily to the increased number of cervicals and decreased number of dorsals, has been still further emphasized by the proportionate length of the individual vertebræ in the two series.

If, as does not seem improbable, the total number of presacrals was ever decreased in any genus it would appear to have been more readily accomplished by the successive elimination of the less specialized, or at least more simple, anterior cervicals than by the disappearance of the extremely complicated dorsals. Nor does it seem probable or even possible that such a decrease in the number of presacrals could have been brought about by the gradual shifting of the pelvic girdle to a more anterior position. Such an hypothesis presupposes the addition to the sacrum of successive posterior dorsals and the liberating of posterior sacrals as anterior caudals, an hypothesis which to the present writer appears unworthy of serious consideration. As to the total number of caudals in the present genus we have nothing upon which to base anything like a reliable estimate. From the character of the posterior five or six of the series of nineteen anterior caudals in the type of *H. priscus* we may judge that while the tail was relatively short the number of caudals was considerable and probably not less than forty. The increased number of caudals is indicated in the first place by the character of the chevron found attached to the thirteenth caudal and which, as already remarked, resembles in general form the chevron of a caudal occupying a more anterior position in *Diplodocus*. Moreover, the very gradual change which is seen to be taking place in the posterior caudals of the series preserved in the type of *H. priscus* indicates a very considerable number of posterior caudals as having intervened between the last of the series and the end of the tail. The extreme shortness of the centra in the caudals of *Haplocanthosaurus* may be considered as sufficient proof that the tail was proportionately rather short as compared with that of *Diplodocus*.

After a careful consideration of all the evidence at hand the following is submitted as the approximate vertebral formula in the present genus. *Cervicals 15; Dorsals 14; Sacrals 5; Caudals not less than 40.*

Below I give the principal dimensions of the several vertebræ pertaining to the type of the present species. Some of these dimensions have been materially altered by crushing in such manner as to cause apparent inconsistencies. They should only be taken as representing in a general way the dimensions of the various vertebræ.

In column 1 the greatest expanse of the transverse processes is given, column 2, greatest length of centrum; column 3, transverse diameter of centrum at posterior extremity; column 4, hight of neural spines above middle of inferior border of centra in presacrals and above inferior border of posterior end in postsacrals.

	1.		2.		3.		4.	
	mm.	in.	mm.	in.	mm.	in	mm.	in.
4. Cervical.	154	$6\frac{1}{16}$	143	$5\frac{5}{8}$	61	$2\frac{3}{8}$	136	$5\frac{3}{8}$
8. "	210	$8\frac{1}{4}$	220	$8\frac{5}{8}$	103	4	192	$7\frac{1}{2}$
9. "	?	?	?	?	?	?	?	?
10. "	192	$7\frac{1}{2}$	243	$9\frac{1}{2}$	102	4	196	$7\frac{3}{4}$
11. "	204	8	238	$9\frac{3}{8}$	111	$4\frac{3}{8}$	225	$8\frac{7}{8}$
12. "	234	$9\frac{1}{4}$	264	$10\frac{1}{4}$	113	$4\frac{3}{8}$	255	10
13. "	258	$10\frac{1}{8}$	292	$11\frac{1}{2}$	125	$4\frac{7}{8}$	265	$10\frac{7}{16}$
14. "			268	$10\frac{1}{2}$	112	$4\frac{3}{8}$		
15. "	320	$12\frac{1}{2}$						
2. Dorsal.	390	$15\frac{1}{4}$	200	8	125	$4\frac{7}{8}$	368	$14\frac{1}{2}$
3. "	374	$14\frac{3}{4}$	120	$4\frac{3}{4}$	127	5	422	$16\frac{5}{8}$
4. "	395	$15\frac{5}{8}$	150	$5\frac{7}{8}$	115	$4\frac{1}{2}$	435	$17\frac{1}{8}$
5. "	390	$15\frac{3}{8}$	135	$5\frac{1}{4}$	124	$4\frac{3}{8}$	483	19
6. "			150	$5\frac{7}{8}$	109	$4\frac{1}{4}$	492	$19\frac{3}{8}$
7. "			135	$5\frac{1}{4}$	116	$4\frac{9}{16}$	500	$19\frac{3}{4}$
8. "			170	$6\frac{5}{8}$	102	4	550	$21\frac{5}{8}$
9. "			152	6	137	$5\frac{3}{8}$	540	$21\frac{1}{4}$
10. "			148	$5\frac{3}{4}$	145	$5\frac{9}{16}$	558	22
11. "			143	$5\frac{5}{8}$	175	$6\frac{7}{8}$	535	21
12. "			137	$5\frac{3}{8}$	169	$6\frac{5}{8}$	549	$21\frac{9}{16}$
13. "			135	$5\frac{5}{16}$	178	7	560	22
14. "			125	$4\frac{15}{16}$	170	$6\frac{3}{4}$	552	$21\frac{3}{4}$
1. Caudal.	350	$13\frac{3}{4}$	115	$4\frac{1}{2}$	160	$6\frac{7}{8}$	425	$16\frac{3}{4}$
2. "	310	$12\frac{1}{4}$	80	$3\frac{1}{8}$	166	$6\frac{1}{2}$	410	$16\frac{1}{8}$
3. "			75	3	165	$6\frac{1}{2}$	393	$15\frac{1}{2}$
4. "			83	$3\frac{1}{4}$	157	$6\frac{1}{4}$	355	$14\frac{3}{8}$
5. "			83	$3\frac{1}{4}$	143	$5\frac{5}{8}$	346	$13\frac{5}{8}$
6. "			90	$3\frac{1}{2}$	130	$5\frac{1}{8}$	331	13
7. "			85	$3\frac{3}{8}$	133	$5\frac{1}{4}$	313	$12\frac{1}{4}$

The Pectoral Arch. (Figs. 17, 18, 19.)

Only the left scapula (Figs. 17 and 18) and right coracoid (Fig. 19) are preserved.

The Coracoid (Fig. 19). — The external surface of this bone is regularly but gently convex. The internal surface is concave. The anterior and inferior margins are for the most part thin, but at the antero-inferior angle the margin is thickened and presents an elongated rugosity shown at *a* 140 mm. in length and 40 mm. in greatest breadth, probably for the ligamentous articulation of the sternum. The surface for articulation with the scapula has a length of 150 mm. and a greatest breadth, at its junction with the glenoid border, of 90 mm. The coracoid forms about one half the glenoid cavity and the glenoidal surface meets the surface for articulation with the scapula at an obtuse angle. Between the inferior margin of the glenoid cavity and the inferior border there is a rather deep notch in the posterior border of the coracoid. The foramen is large and is situated about 35 mm. beneath the coraco-scapular suture. It is elliptical in outline with the vertical diameter the longer. The dimensions are 57 mm. for the vertical and 30 mm. for the transverse diameter at the external opening. The distance from the glenoid border to the sutural surface at the antero-inferior angle is 295 mm. The distance from the postero-inferior angle to the anterior border just beneath the coraco-scapular suture is 350 mm.

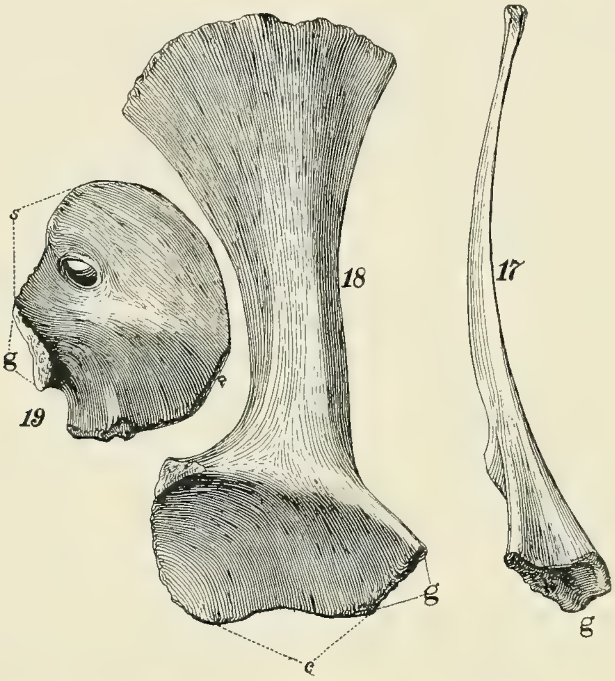


FIG. 17. Posterior view of left scapula of *H. utterbacki*; *g*, glenoid surface, $\frac{1}{10}$ natural size.

FIG. 18. External view of same; *g*, glenoid surface; *c*, surface for coracoid.

FIG. 19. External view of right coracoid of *H. utterbacki*; *s*, surface for scapula; *g*, glenoid surface; *a*, rugosity for supposed contact with sternal, $\frac{1}{10}$ natural size.

The Scapula (Figs. 17 and 18). — The scapula displays the extreme development of that form shown in *Morosaurus* with broadly expanded extremities. I cannot describe the characters better than to give the measurements. The breadth of the scapula at the proximal end is 372 mm., at the distal[6] 396 mm. and in the middle only 137 mm. Between the spine and the coraco-scapular suture there is a broad but shallow cavity on the external surface of the scapula. Above this ridge, however, the external surface of the scapula is convex in all directions. The total length of the scapula from its superior or proximal end to the coraco-scapular suture is 800 mm. The accompanying figures show very well the form and principal characters of this element.

From the foregoing description of the types of the two species of *Haplocanthosaurus* at present known and from the accompanying measurements and figures it will appear that as compared with *Diplodocus* the present genus was represented by animals with the thorax somewhat more elongated and with neck and tail relatively shorter than those which obtained in representatives of the former genus. While, judging from the femur, the only element of the limbs at present available, the appendicular skeleton was relatively strong when compared with the axial.

Distinctive Generic Characters.

The principal characters distinguishing the genus *Haplocanthosaurus* may be summarized as follows:

FIRST. — *Neural spines short and simple (not branched) throughout the entire vertebral column.*

SECOND. — *Neural spines of the anterior sacrals coössified, forming an elongated bony plate.*

THIRD. — *Height of neural arches in posterior dorsals exceeding length of neural spines.*

FOURTH. — *Transverse processes of the anterior and mid-dorsal regions inclined upward and outward instead of directly outward.*

The two species described above may be distinguished as follows by their respective sacra.

HAPLOCANTHOSAURUS PRISCUS. — *With neural spines of the three anterior sacrals coössified, those of the two posterior remaining free.*

HAPLOCANTHOSAURUS UTTERBACKI. — *With neural spines of the four anterior sacrals coössified throughout their entire length and with that of the fifth sacral at the top and bottom.*

Taxonomy.

All systematists will, I think, agree with me in placing the present genus among the *Sauropoda.* The scapula, coracoid, pelvis and sacrum, as well as the presence of large pleurocentral cavities in the presacral centra, together furnish conclusive evidence as to its affinities with that group of the *Dinosauria.* Nevertheless there are a few characters, such as the elongated neural arches and comparatively short and absolutely simple neural spines of the dorsal and posterior cervical series, the conformation of the transverse processes and position of the capitular rib facets, which are different from any other known member of the *Sauropoda* of North America and are more nearly paralleled by the characters which exist in the vertebræ of this region in some members of the *Predentata,* more especially in *Stegosaurus,* where, as in *Haplocanthosaurus,* the neural spines are short as compared with the elevated neural arches from the summit of which, in each case in the posterior dorsals, the transverse processes spring and diverge from the bases of the perpendicular spines at angles of about 45° instead of being directed horizontally as is the usual manner in the *Sauropoda.* The presence of characters so similar as those just mentioned in representatives of the *Sauropoda* and the *Predentata* while certainly not indicative of any very close relationship may perhaps be considered as evidence of a remote common ancestry for the two groups. If this view be taken, these characters possessed in common would be considered not as parallel or analogous characters developed independently in each instance, but as persistent primitive characters which were present in their remote but common ancestors. As the development of the two groups progressed and they became more and more differentiated, such characters proved advantageous and became more emphasized in the *Predentata* while in the *Sauropoda,* where for some reason they were not particularly advantageous, they were gradually eliminated and disappeared altogether in the more highly specialized forms though persisting in the more primitive *Haplocanthosaurus.* It is by the presence in common, among the *Sauropoda, Theropoda* and *Predentata,* of such characters as those just described, that the student of the Dinosauria will find the most trustworthy evidence as to the actual relationships or want of relationships in the three groups. Not until a considerable number of genera within each group are known from a detailed study of the osteology of fairly complete skeletons will it be possible to pronounce with any degree of certainty even upon the question as to whether the Dinosauria is a natural group as maintained by Marsh or an entirely unnatural one, without any right to existence, into which has been thrown three distinct groups, totally dissimilar and with nothing in common, as was held by the late Dr. George Baur. In the discussion of this question however there are several points which should be constantly kept in mind by the advocates of either view. Among these are:

---

[6] I consider that end of the scapula which opposes the humerus as the distal.

First.— Those who are opposed to considering the *Dinosauria* as a natural group should bear in mind the great antiquity that must be accorded to that group when considered as constituting a single group. Evidence of such antiquity is found not alone in the great diversity exhibited by the three subdivisions into which the group as a whole has been divided but by the diversity and specialization exhibited by the different families, genera and species within each of these three subdivisions, As yet we know comparatively little of the earlier *Dinosauria* and the group if in reality it be a natural one is at present represented in our museums for the most part only by the later and more specialized forms. Of the *Sauropoda* we know only those forms which lived just prior to their extermination when they were already highly specialized. Consider for a moment the enormous time interval which must have been necessary for the development of a reptile like *Diplodocus.* Yet his remains are found associated in the same quarry with those of *Haplocanthosaurus.* the most primitive Sauropod known, and the entire range of the Sauropoda throughout the geological column in North America so far as at present known is limited to certain horizons in the Jurassic or Lower Cretaceous of some authors, with a vertical thickness never exceeding a few hundred feet, and from the top to the bottom of which there are always found forms which are highly specialized, conclusive proof that the paleontological record is exceedingly incomplete as regards this group.

Although the time distribution of the *Theropoda* and *Predentata* as we now know it is more considerable than that of the *Sauropoda* yet it is by no means complete and we know little of the earlier forms of either of these divisions. The wonder therefore is not that the three divisions as we now know them should show so little in common, but rather that, considering their great antiquity and early differentiation, they should have continued to possess in common even such characters as they do show.

Second.—Although due weight should be given to every marked and important difference in structure it should nevertheless be borne in mind that every character possessed in common by these three divisions or by any two of them should be considered as an evidence of relationship until definitely proved to be fortuitous or as having been developed independently in each instance.

Third.—It is in the, as yet undiscovered, earlier and more generalized members of these groups that we must look for those characters which will throw most light on this question. If future explorations should be rewarded by the discovery in the early or middle Trias of a considerable number of representatives of each of the groups which we now refer to the *Dinosauria,* and if together they were shown to possess many characters in common and to approach one another much more nearly than do the Jurassic and Cretaceous forms, this evidence would be considered as strongly favoring the including of them all in a single group, the *Dinosauria.* If on the other hand they were found to show little in common or were even more widely separated than are the later forms from the Jurassic and Cretaceous then there could be no reasonable grounds for considering the Dinosauria as a natural group and it would become necessary to discard that term, at least in the sense in which it is at present used.

Since however as has been shown in *Haplocanthosaurus*, the *Sauropoda* and *Predentata* do possess certain important anatomical characters in common and since in this the most generalized genus of the group at present known the relationships between these two groups are more apparent than in the more specialized genera, *Diplodocus, Brontosaurus*, etc. It is reasonable to suppose that in the yet undiscovered but still more generalized forms greater similarity in structure will be found. Moreover from our present knowledge the relationships between the *Sauropoda, Predentata* and *Theropoda*, as has already been pointed out by Marsh, is indicated by a number of important characters possessed in common such as:

"1. *Teeth with distinct roots either fixed in more or less distinct sockets or in longitudinal grooves, never ankylosed, no palatal teeth.*

"2. *Skull with superior and inferior temporal arches.*

"3. *Double-headed cervical and thoracic ribs.*

"4. *Sacral vertebræ coössified and more numerous than in other reptiles, seldom less than five.*

"5. *Ilium extended in front of acetabulum, in the construction of which latter the ilium, ischium and pubis take part.*

"6. *Fibula complete.*

"7. *The reduction in the number of digits commences with the fifth.*"

The present author is, therefore, of the opinion that the Dinosauria should be regarded as a valid and distinct group for the exact definition and description of which we must await further discoveries as also for definite proof that the different groups now included in it are actually related.

Admitting that the Dinosauria do constitute a natural group we have next to consider the rank that should be accorded to it in any general scheme looking to a classification of the Animal Kingdom as a whole. Here again we find there has been great diversity of opinion. Without reviewing the various opinions that have at various times been expressed upon this subject it would appear to the present author, that, in consideration of the diversity in form, structure and habit which are found withing this group where some members are carnivorous and others herbivorous, some quadrupedal and others bipedal, some heavily armored and others un-armored and with all the many and diverse anatomical characters shown in their osteology which might reasonably be expected from such diversity of habits, there would seem good reasons for considering the Dinosauria as deserving of the rank of a subclass of the Reptilia comparable for example with the Metatheria of the Mammalia and divisible into three orders for each of which several names have been proposed by various authors. Of all these, those proposed by Marsh appear to the present writer to be the most appropriate, these are:

1. THE THEROPODA; *Embracing all the carnivorous dinosarus.*
2. THE SAUROPODA; *Embracing all the herbivorous forms in which the predentary is wanting.*
3. THE PREDENTATA; *Embracing all the herbivorous forms in which the predentary is present.*

In accepting the terms *Theropoda* and *Sauropoda* rather than *Megalosauria* and *Cetiosauria* I do so out of regard for the more comprehensive nature of those terms as used by Marsh. The latter terms as used originally by Fitzinger (*Megalosauri*), 1843, and Seeley, 1874, respectively, I consider of subordinal rank only. *Predentata*, Marsh, is preferable to *Orthopoda*, Cope, because it is in no sense coördinate with the latter but a much more comprehensive term. Cope's *Orthopoda* and the *Ornithopoda* of Marsh (not Huxley) are more nearly synonymous.

Some authorities have considered the *Sauropoda* of Marsh (1878) as a synonym of the *Opisthocœlia* of Owen (1859). But this appears to me quite unwarranted. For the latter term, although having priority, was never adequately defined by Owen. It was originally proposed as a suborder of the *Crocodilia*[7] and was characterized as embracing members of that group with opisthocœlous dorsal and cervical vertebræ. Owens' original definition of the *Opisthocœlia* was as follows: "The small group of *Crocidilia*, so called, is an artificial one based upon more or less of the anterior trunk vertebræ being united by ball-and-socket joints, but having the ball in front, instead of, as in modern crocodiles, behind." As is now well known, the above character in no way distinguishes these dinosaurs from members of either the *Theropoda* or *Predentata*, and on the same page, in defining the order *Dinosauria*, Owen describes the cervical vertebræ as being opisthocœlous in some species. It is thus clear that Owen not only did not adequately define his proposed suborder *Opisthocœlia*, but that he did not recognize its real relationships as being with the *Dinosauria* rather than the *Crocodilia*. The character given distinguishes it from the *Procœlia* or true *Crocodilia*, but should be considered as uniting it with, rather than separating it from, the Theropod and Predentate dinosaurs, for as has already been stated this character is possessed in common by members of both these groups. While *Cetiosaurus* is an undoubted member of the *Sauropoda* (Opisthocœlia) as determined by Owen, this fact does not serve to define properly the latter term which remains a *nomen nudum*, while the *Sauropoda*, proposed and defined by Marsh in the *American Journal of Science* for November, 1878, page 412, should be accepted as the first adequately defined name for this group of dinosaurs.

---

[7] See Report 29th meeting Brit. Assoc. Adv. Sci., 1859, pp. 164, 165.

In proposing the term Sauropoda for this group of dinosaurs in the paper just cited Marsh adds:

"The most marked characters of this group are as follows:

"1. The fore and hind limbs are nearly equal in size.

"2. The carpal and tarsal bones are distinct.

"3. The feet are plantigrade, with five toes on each foot.

"4. The precaudal vertebræ contain large cavities, apparently pneumatic.

"5. The neural arches are united to the centra by suture.

"6. The sacral vertebræ do not exceed four, and each supports its own transverse process.

"7. The chevrons have free articular extremities.

"8. The pubes unite in front by ventral symphysis.

"9. The third trochanter is rudimentary or wanting.

"10. The limb bones are without medullary cavities."

Although the subsequent discovery of more complete material has shown that No. 6 of these characters is erroneous, and that certain others are possessed in common by some members of the Theropoda and Predentata, yet Marsh's original definition still remains fairly diagnostic of the group, and the term *Sauropoda* should, therefore, it appears to the present writer, be accepted.

Whether this group should be considered as of only subordinal rank, as originally proposed by Marsh or as of ordinal value as considered in his later publications, is a question concerning which there is at present no unanimity of opinion. Each student must, for the present at least, determine for himself the rank to be assigned such groups, and such decisions will necessarily be determined by, and vary according as certain characters are considered as of greater or less importance by the different investigators. Without going into an extended discussion of this question the present author feels warranted in considering the *Sauropoda* as a distinct order, comparable for instance with the Ungulata among the Eutherian Mammalia, or the Diprodontia among the Metatheria, according to Gadow's "Classification of the Vertebrata."

It now remains to discuss the relations of the genus *Haplocanthosaurus* to the various genera and families of the Sauropoda that have already been proposed.

This will be the more easily understood if we first notice briefly the principal characters of the different families within that order.

Marsh has divided the Sauropoda into six families which he has named as follows: (1) *Atlantosauridæ;* (2) *Diplodocidæ;* (3) *Morosauridæ;* (4) *Pleurocœlidæ;* (5) *Titanosauridæ;* (6) *Cardiodontidæ.*

As already stated in my memoir on *Diplodocus*, when discussing the taxonomy of that genus, it is not improbable that the number of families recognized by Marsh is too great and should be somewhat reduced. However it would seem premature to attempt a revision of the genera and families of this group until the large and splendid collections recently brought together by the Carnegie Museum, the American Museum and the Field Columbian Museum have been thoroughly studied. It is safe to say, however, that no such reduction in the number of families as that proposed in the second volume of the English edition of Zittel's "Text-Book of Paleontology" will become necessary. Nor will it be found necessary or desirable to associate in the same family genera so different as are *Brontosaurus* and *Morosaurus* as was done in the volume just cited.

From the foregoing description of the types of *Haplocanthosaurus priscus* and *H. utterbacki* it will readily appear that the affinities of that genus are with the *Morosauridæ.* The relationships with that family are shown by the expanded superior extremity of the scapula; the general form of the different pelvic elements, more especially the pubes and ischia; the simpler structure of the presacral vertebræ; the short spines of the dorsals and sacrals; the biconcave centra of the caudals and in the relative breadth and height of the sacrum. While the relationships with the *Morosauridæ* are clearly indicated by the presence of these and other characters of scarcely less importance, yet there are present certain characters even more marked than most of those which at present serve to distinguish even the most widely separated families of the *Sauropoda* now known. These are the perfectly simple neural spines of the anterior dorsals and posterior cervicals; the different position in the sacrum of the sacrals with coössified sacral spines; the greater number of dorsal vertebræ and the much simpler structure of the individual vertebræ throughout the entire vertebral column. Such differences as these will doubtless be considered by some as of family or at least subfamily importance. Since, for the most part at least, they are only such differences as we might reasonably expect to find among the more primitive and less highly specialized members of that family I prefer to regard *Haplocanthosaurus* as pertaining to the *Morosauridæ* and including species the most generalized of any yet known in that or any other family of the Sauropoda.

It is easy to see how the slight emarginations at the summit of the neural spines in the anterior dorsals and posterior cervicals of *H. utterbacki* might become successively more and more emphasized until they became actually bifid, at least to the extent that obtains in *Morosaurus*. Nor is it impossible that while specialization was taking place along this particular direction, the centra, transverse processes, etc., may have assumed a more and more complicated structure. It is by some such process as this that the present author conceives that *Morosaurus* was developed from some earlier and more primitive form which was alike ancestral to that genus and *Haplocanthosaurus*, the latter, however, being less progressive than the former, became less modified and preserves more nearly the general form and character of their common ancestral stock.

Although representatives of both genera lived contemporaneously, as is shown by the presence of undoubted remains of both in the Canyon City quarry, it is more than probable that *Morosaurus* long survived the other since remains of that genus are abundant near the top of the Jurassic in southern Wyoming while as yet no remains of *Haplocanthosaurus* are certainly known to have been obtained there.

RELATIONS OF HAPLOCANTHOSAURUS TO EUROPEAN AND SOUTH AMERICAN FORMS.

As yet we have only discussed the relations of the present genus with North American representatives of the Sauropoda. It now remains to notice briefly the relations of this genus with certain forms from Europe and South America with which it seems to show some relationships.

Chondrosteosaurus compared with Haplocanthosaurus.

The characters exhibited by the vertebral centra of *Haplocanthosaurus* are somewhat similar to those shown in *Chondrosteosaurus gigas* Owen, founded on the centrum of an anterior dorsal or cervical vertebra from the Wealden of the Isle of Wight and described and figured in *Supplement (No. VI.) to the Monograph of the Fossil Reptilia of the Wealden and Purbeck Formations; pp. 5 to 7, Plates II–V, of Owen's British Fossil Reptiles, London, 1876.*

This resemblance is especially apparent in Plate II., Fig. 2, and Plate V., Fig. 1 of the paper just cited. However the resemblances shown are not of a character which would indicate a closer relationship between *Chondrosteosaurus* and *Haplocanthosaurus* than between the former of these with any one of several other genera of the Sauropoda. Nor is it possible, owing to the fragmentary nature of the material upon which that genus was based, to decide with certainty even as to just what family of the Sauropoda it pertained, although Owen's statement that the transverse diameter of the centrum exceeds the vertical together with the broad, almost flat inferior surface and other characters indicated by the figures would seem to fix this centrum as pertaining to a median cervical of some member of the *Morosauridæ.*

Comparison of Haplocanthosaurus with Bothriospondylus Owen.

A comparison of the various characters exhibited by the species of *Bothriospondylus* described by Owen in his Monograph on that genus published as part II., of his *Reptilia of the Mesozoic Formations*, pp. 15–26, Plates III.–IX., will show many striking resemblances to *Haplocanthosaurus* and at first sight one might be led to believe that they pertain to the same genus as that to which the material under discussion pertains. A closer examination however will reveal several striking and important differences certainly to be regarded as of generic if not of family rank. Such distinctive characters are especially observable in the sacral centra as will be seen by a comparison of Fig. 20 showing side views respectively of the fourth and terminal sacral centra of the type of *Haplocanthosaurus utterbacki* with the figures on Plates III. and IV., of the monograph just cited. As will be seen by an examination of Owen's figures and text the median sacrals of *Bothriospondylus* are provided with both anterior and posterior parapophysial facets, while in *Haplocanthosaurus* as shown in Fig. 20, there is but a single facet, which in the centrum of the fourth sacral is median in position antero-posteriorly, but somewhat elevated above the median longitudinal line. Furthermore the pleurocentral cavities so conspicuous in the sacral centra of *Haplocanthosaurus* beneath the parapophyses are entirely wanting in *Bothriospondylus.* The cavities in the sacrals of that genus shown at *f*, Plate III., Figs. 2 and 4, and Plate IV., 4 and 5, of Owen's Monograph lie above the parapophyses and are not homologous with the pleurocentral cavities. These characters as well as others of only less importance are quite sufficient to distinguish *Haplocanthosaurus* from *Bothriospondylus.*

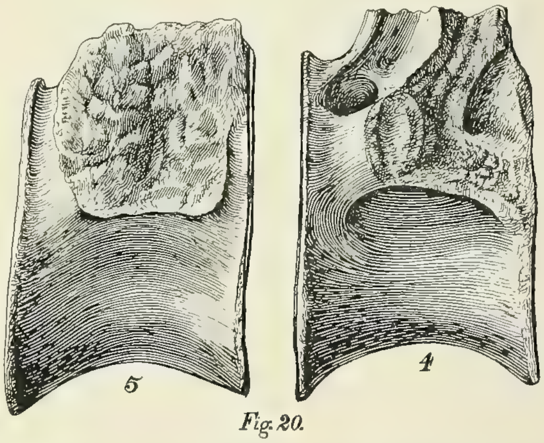
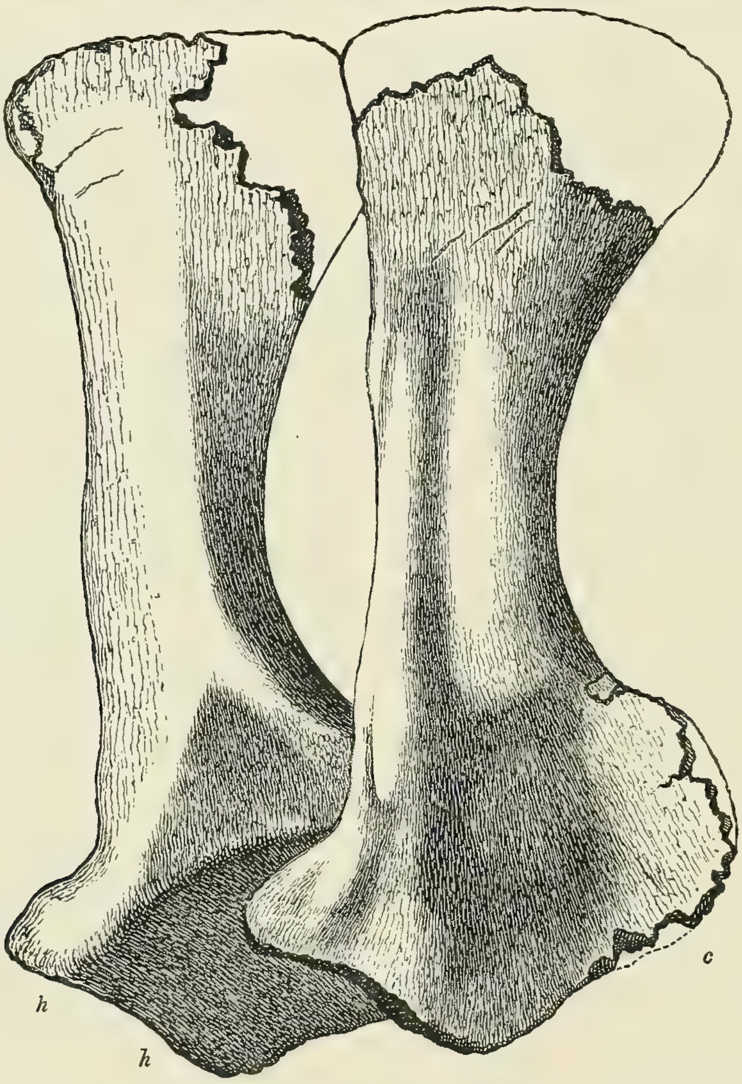


FIG. 20. 4. Centrum of fourth sacral of *Haplocanthosaurus utterbacki* seen from right side (No. 879). 5. Same view of fifth or last sacral centrum of same. Both $\frac{1}{4}$ natural size.

Comparison of Haplocanthosaurns with Cetiosaurus Owen.

Of all the British representatives of the *Sauropoda* perhaps the most striking resemblances to *Haplocanthosaurus* are to be found in *Cetiosaurus longus* Owen, as shown in remains representing a considerable portion of a single skeleton discovered in 1868–70 in quarries of the Great Oolite of Enslow Rocks at Kirtlington Station, eight miles north of Oxford, and showing so close a resemblance to the type of *C. longus* that it was used by Owen in his detailed description of that species in his *Monograph on the genus Cetiosaurus in Part II. of his British Fossil Reptiles of the*



Right. **Left.**

FIG. 21. Scapulæ of *Cetiosaurus longus* Owen, after Owen, $\frac{1}{10}$ natural size; *hh*, surface for articulation with humerus; *c*, surface for articulation with coracoid.

Mesozoic Formations, pp. 25–43, Plate X., text figures 1–10. The resemblances in these two forms are very numerous and are to be seen in the scapulæ, as compare Figs. 18 and 21; the femur, the ilium and the vertebræ as figured and described by Owen in his Monograph. Indeed, if the vertebra described as an anterior dorsal in the last paragraph on page 29 of his monograph is really an anterior dorsal this resemblance would seem to be more than superficial, for according to Owen's description the neural spine seems to be quite simple and the diapophyses are described as being directed upward and outward at an angle of 45° with the neural spine, characters precisely like those already described as obtaining in *Haplocanthosaurus.* Unfortunately Owen does not figure this vertebra, and were it not for the fact that he describes it as being massive, one might readily believe on the evidence of this vertebra alone that it pertained to a genus closely related to or identical with those remains which I have made the type of *Haplocanthosaurus.* However the vertebræ of *Haplocanthosaurus* can by no means be considered massive when compared with the vertebræ of other members of the Sauropoda. Moreover, in *Haplocanthosaurus* the vertebræ show numerous large intra-mural cavities instead of the close, though cancellous texture of these bones, resembling that which obtains in the whales, which is present in the British genus and which suggested the generic name *Cetiosaurus.* This difference in character would seem a very important one, if it were shown to exist in those vertebræ of *Cetiosaurus* which are most cavernous in *Haplocanthosaurus.* There are, however, other and quite striking differences, notwithstanding the general similarity in the osteology of these two genera. The coracoid, according to Owen, is especially different, as will be apparent after a comparison of Figs. 19 and 22. If Owen's figure is correct the coracoid of Cetiosaurus is without a foramen, a character which, if correct, is entirely unique, in so far as I am aware, among not only the Sauropoda but the herbivorous dinosaurs generally. It appears to me quite possible that Owen's figure is erroneous and that the coracoid is so distorted or imperfect as not to show a foramen in the example from which his drawing was made. It does not seem possible that such a striking difference could normally have existed in the coracoids of two genera otherwise so

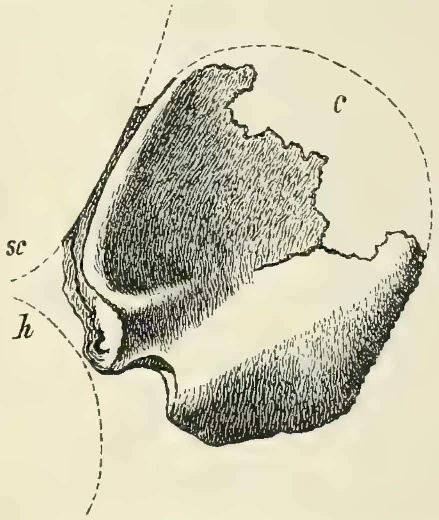


FIG. 22. Coracoid of *Cetiosaurus longus* Owen, after Owen. $\frac{1}{10}$ natural size. *sc*, surface for scapula; *h*, surface for humerus.

closely related as these genera appear to be and I would suggest a reëxamination of the British specimen by those who may have access to it. While *Haplocanthosaurus* and *Cetiosaurus* are certainly generically distinct I believe they may pertain to the same family.

Although there are undoubted close similarities in structure between *Haplocanthosaurus* and the three genera of British Sauropods mentioned above, yet, if we can rely upon the characters represented by a single vertebra, it is in South America that there has been found the remains of a Sauropod dinosaur showing the closest relations with this genus. I refer to the dorsal vertebra recently described and figured by F. Baron Nopsca [8] and provisionally referred by him to *Bothriospondylus.* From Nopsca's figures, it will be seen that from the material at hand it is not generically distinguishable from *Haplocanthosaurus* the corresponding vertebra of which it resembles very closely. Note for instance the simple neural spine, elevated diapophyses, high neural arches, reduced centra, character and arrangement of the various laminæ, position and character of the tubercular and capitular rib facets, all of which are characters similar to, indeed almost identical with, those found in the median dorsals of *Haplocanthosaurus.* Without claiming that the two are undoubtedly congeneric I wish to emphasize the very striking similarity in structure which they exhibit.

From the above study of the material constituting the types of *Haplocanthosaurus priscus* and *H. utterbacki* the present author feels justified in regarding that genus as representing the least specialized member of the Sauropoda yet discovered. Of the families of Sauropoda already proposed its closest affinities are undoubtedly with the *Morosauridæ* and I prefer to include it in that family rather than to erect for it a new family, although some will doubtless think it deserving of the rank of a distinct family, the *Haplocanthosauridæ.* According to that classification of the Dinosauria which it appears to me is most acceptable, considering our present knowledge of the group, the taxonomy of *Haplocanthosaurus* would be best expressed by considering it as a well-marked genus of the family *Morosauridæ* of the order Sauropoda, subclass Dinosauria, class Reptilia.

Probable Habits of the Sauropoda.

Great diversity of opinion has been expressed by various authors regarding the habits of the different genera of Sauropod dinosaurs. Owen, on page 39 of his "Fossil Reptilia of the Great Oölite," speaks as follows of the probable habits of these giant reptiles. "These enormous *Cetiosauri* may be presumed to have been of aquatic and, most probably, of marine habits. . . ." Seeley[9] at one time considered representatives of the genus *Bothriospondylus* (*Ornithopsis*) as "*clearly ornithic*" and this idea suggested to him the name *Ornithopsis* for those reptiles.

---

[8] Sitzungsberichten der kaiserl. Akademie der Wissenschaften in Wien. Mathem. naturw. Classe, Bd. CXL., Abth. 1, Feb., 1902, pp. 108–114.

Osborn in his memoir entitled "A Skeleton of Diplodocus" leans to the aquatic habits of these reptiles, holding that the tail is especially modified to function as a swimming organ and was provided distally with a "vertical fin"! He believes the chief function of the tail to have been that of a propeller to aid the animal in swimming and that it functioned secondarily as a balancing and supporting organ. While holding that the Sauropoda (Cetiosaurs) are aquatic and quadrupedal, he infers that they were capable of migration on land and of assuming both a bipedal and tripodal position, the tail when in the latter position functioning as a third support in conjunction with the hinder pair of legs.

Marsh was the first to advance the aquatic habits of *Diplodocus*, having considered the position of the narial opening as suggestive of such habits. In his memoir on *Diplodocus* the present author accepted an aquatic life as that to which representatives of that genus seemed best adapted when considered from their anatomical structure as a whole. I remarked in that connection "That I was inclined to the opinion that *Diplodocus* was essentially an aquatic animal, but quite capable of locomotion on land."

So similar in general form and anatomical characters are the different genera of the Sauropoda that we may consider the group as a whole as a remarkably homogeneous one, with quite similar though not identical habits characterizing most if not all of its representatives. It would seem therefore more advantageous to discuss the probable habits and mode of life of the group as a whole than those of any particular genus. In any such discussion there are several classes of facts from which evidence more or less important can be obtained bearing upon the subject. Among these may be mentioned the following:

1. *The anatomical or osteological characters of the group.*
2. *The nature of the other associated fossils including vertebrates, invertebrates and plants.*
3. *The condition in which the remains are found imbedded in the matrix.*
4. *The nature of the matrix in which the remains are found.*

Let us next consider in the order enumerated above the evidences afforded as to the life habits of the Sauropoda by these four classes of testimony.

First: As to the evidence furnished by the osteological and anatomical characters of the Sauropoda. As already observed, Marsh has considered the elevated position of the anterior nares in *Diplodocus* as evidence of an aquatic life. But this evidence, although strongly presumptive, is by no means conclusive, for there are among living terrestrial vertebrates similar conditions, more especially among the mammalia accompanied by habits which are in no sense aquatic, while such essentially aquatic or amphibious reptiles as the crocodiles, alligators and gavials have the narial opening in its normal position at the distal extremity of the snout. In like manner Owen's remark that, "These enormous *Cetiosauri* may be presumed to have been of aquatic and, most probably of marine habits, on the evidence of the coarse cancellous tissue of the long bones which show no trace of medullary cavity" is not conclusive since some of the most strictly aquatic reptilia and mammalia, as for instance the Manatee among the latter class have exceptionally dense and heavy bones. However this exception is not so important, as it might at first glance seem to be, for it is a well-known fact that in the Manatee the bones have acquired greater density and increased specific gravity in order to aid these animals in retaining a submerged position while feeding on the aquatic plants found growing on the bottom of the shallow waters in which they live. It is clear that the feeding habits of the Sauropoda required no such modification of the osseous skeleton, and that if modified at all for aquatic habits, it was in the direction of a more open and cancellous structure even than that which obtains in the Cetacea and calculated not only to give greater buoyancy to these massive quadrupeds when in water but, in addition, to give the greatest possible surface for muscular attachment compatible with the required rigidity and with the least possible weight. As Osborn, in speaking of the axial skeleton of *Diplodocus,* has truly remarked "*It is a mechanical triumph of great size, lightness and strength.*" Although the present writer cannot agree with Osborn in considering the chief function of the tail as that of a swimming organ, even in *Diplodocus* the most highly specialized member of the order, with the probable exception of *Barosaurus;* and while there seems to be no evidence whatever of the presence of a vertical fin on the tail of that genus as suggested by Osborn, I nevertheless believe that all the Sauropoda were aquatic to the extent that they frequented swamps, marshes, lakes and streams, that they were capable of swimming and that when moving about by that method the tail was a very efficient propelling organ. From the character of the modification of the chevrons of the mid- and posterior caudal regions in all the Sauropoda, however, I believe that when in a normal position, whether on land or in water, the greater portion of the tail rested on the surface of the ground, and I am not prepared to say that its function as a balancing, supporting, or defensive organ, was secondary to its function as a swimming organ. In arriving at any reasonably accurate conception of the habits and usual mode of locomotion of these dinosaurs the structure of the limbs would seem to be of the very first importance although they have not as yet been given more than a passing consideration in this connection. The limbs and feet are now pretty well known in several genera of the Sauropoda and in so far as the Jurassic forms are concerned their structure shows them all to have been strictly quadrupedal, with massive and rather long limbs and feet both behind and in front, the fore limbs with one or two possible exceptions being the shorter. In no instance yet discovered is there any marked or even noticeable tendency toward abbreviating or subordinating the limbs along the lines so universally characteristic of the aquatic or amphibious recent reptilia or mammalia. The structure of the limbs and feet in all the Sauropod genera, where those elements are known, furnish to my mind conclusive evidence that they were first of all ambulatory organs whose usual and normal functions were to give support to the body and enable the animal to walk about over the dry earth or to wade in the shallow rivers, swamps, lakes and other waters while in search of food. When engaged in the latter occupation their great size aided by their long necks would enable them to essay waters of no inconsiderable depth with little inconvenience.

---

[9] "On Ornithopsis, a gigantic animal of the Pterodactyle kind, from The Wealden." *Annals and Mag. of Nat. Hist.*, 1870, p. 279.

Second: As to the character of the associated fossils.

Wherever remains of Sauropod dinosaurs have been found in this country, there has been found associated with them in more or less abundance the remains of Theropod and Predentate dinosaurs. The classic quarry near Canyon City, Colorado, where the types of the two species of *Haplocanthosaurus* described above were found has also yielded remains of *Diplodocus*, *Brontosaurus*, *Morosaurus*,, *Ceratosaurus*, *Allosaurus*, and *Stegosaurus*, besides other dinosaurs, crocodiles, turtles, fishes and diminutive mammals all from the immediate sandstones in which the dinosaurs occur. While in the adjacent clays there are numerous small lenticular masses of limestone abounding in fresh-water gasteropods and remains of small fresh-water plants. And in the clays themselves at a few especially favored localities the shells and casts of several species of *Unio* occur in great abundance. The character of the fauna and limited flora found associated with these dinosaurs, whether considered individually or as an assemblage is not what would be regarded as strictly aquatic. Such aquatic forms as are found like the bivalves, gasteropods, fishes, turtles and crocodiles indicate for the most part shallow waters or at least streams and lakes of only moderate extent and depth.

Third: The condition of the remains as they lay imbedded in the matrix will afford some evidence as to the habits of the Sauropoda, for it is evident that if these ponderous reptiles were actually aquatic they would require bodies of water of no inconsiderable dimensions and depth for their accommodation and it is not at all reasonable to suppose that when overtaken by death either through disease, old age or the attacks of their enemies they would seek other than their natural habitat. Therefore if they lived and died in deep water, after death it is only natural to suppose that their carcasses would sink to the bottom and become buried beneath the accumulating sands and clays with the different bones of the skeleton still in their proper positions relative to one another. For among the strictly aquatic forms (crocodiles, etc.) that lived contemporaneously with them there are none sufficiently large and powerful to disarticulate the skeletons of these gigantic dinosaurs. Since in most instances the skeletons of these dinosaurs are found in even more disarranged and dismembered conditions than were the two described in the present paper it seems far more probable that, as a rule, they have met death in or adjacent to shallow waters, or on land where their carcasses were accessible to the terrestrial carnivorous Dinosauria, to the ravages of which the dismemberment of the skeletons is partially due, as is sometimes evidenced by the tooth marks still preserved on the bones: silent but unmistakable evidences of those prehistoric feasts.

Fourth: The character of the enclosing matrix furnishes important evidence as to the nature of the habitats of those animals whose remains it contains, especially if considered in connection with the character of the surrounding and overlying sedimentary rocks. If as is the case at the quarries near Canyon City, Colorado, the bones are found imbedded in lenticular masses of coarse sandstone showing cross-bedding it is evident that such deposits were laid down in comparatively shallow waters. Furthermore, if as is the case throughout the Jurassic generally, wherever important deposits of dinosaur remains have been found, massive, coarse, or finely bedded sandstones with or without frequent examples of cross-bedding are found replacing the finer, more evenly bedded clays and shales both vertically and laterally even at moderately frequent intervals, it is evident that such beds were not deposited in deep and quite waters; that the immediate region, which by every reasonable presumption should be considered the habitat of the dinosaurs, presented the appearance not of a great sea or lake, but rather of a flat and open country where streams were constantly shifting their courses and the smaller lakes and bayous, though confined within more fixed limits than the streams were not entirely stable. That the country was flat and open rather than mountainous is shown by the absence for the most part, of coarse conglomerates.

Conclusions as to the Habits of the Sauropoda.

In discussing the probable habits of *Diplodocus* in his memoir on that genus, the present author remarked: "I am inclined toward the opinion that *Diplodocus* was essentially an aquatic animal, but quite capable of locomotion on land." I would now after a more thorough study of the osteological characters of several Sauropod genera in connection with more extended geological observations since conducted and bearing upon the probable physiographic features, during Jurassic times, of the regions in which Sauropod remains have been found in more or less abundance, amend this statement of my opinion as follows, making it applicable to the Sauropoda generally.

I believe: *That the Sauropoda were essentially terrestrial reptiles with amphibious habits, passing much, perhaps most, of their time in shallow waters where they were able to wade about in search of food. That their natural and normal mode of progression was ambulatory, as is abundantly evidenced by the structure of their feet and limbs, but that they were quite capable of swimming when through choice or necessity they essayed the deeper waters of the larger lakes and streams, to which they must frequently have been driven to resort for protection from their natural enemies, the contemporaneous carnivorous Theropoda with habits probably still less aquatic than were those of the Sauropoda.*

Origin of the Atlantosaurus Beds.

I have elsewhere (An. Car. Mus., Vol. I., pp. 327–341) described in some detail the geology of the country in the immediate region of the dinosaur quarries near Canyon City, Colorado. It may be of interest in this connection however to describe in greater detail some of the more important quarries of this region, rendered classic by the researches of the late Professors O. C. Marsh and E. D. Cope, and to describe the character of the various strata which in this region constitute that series of sandstones, limestones, shales and marls which together make up the 450 feet of supposedly Jurassic deposits lying between the "Red Beds" below and the Dakota sandstones above. Dr. C. A. White in his article entitled: *Fresh-Water Invertebrates of the North American Jurassic* published as Bulletin 29 of the United States Geological Survey on pages eleven and twelve speaks as follows of these deposits: "The character of the strata in which the fresh-water Jurassic fossils were found, both at the Colorado and the Wyoming localities, in addition to the character of the fossils themselves, is such as to indicate for them a lacustrine and not an estuary or a fluviatile, origin; that is the rocks are regularly stratified and have such an aspect and character as to indicate that they were deposited in one or more large bodies of water. If the strata of the Colorado and of the Wyoming localities really contain an identical fauna, it may be regarded as at least probable that they were deposited in one and the same lake. The distance between the Colorado and the Wyoming localities indicates that the supposed lake was nearly 200 miles across; and, if the Black Hills fossils also belonged to the same contemporaneous fauna, the assumed lake was much larger. The existence of a fresh-water lake of even the smaller size suggested makes it necessary to infer that there was then in that part of the North America of to-day a continental area of considerable size, for such a lake could hardly be other than a part of a large drainage system.

"But aside from these considerations, the existence of such fresh-water faunas as are represented by these collections whether in large or in small bodies of water, indicates with hardly less clearness than the proved existence of one great lake would do the synchronous existence of a large continental area. Indeed it seems necessary to assume that in the fresh waters of a large land area alone, could faunas of such a character as those which are represented by these collections be developed and perpetuated." I can fully agree with Dr. White as to the necessity of assuming the existence in Jurassic times of a continental land-mass of the dimensions intimated in his paper. But it does not seem to me at all necessary to presuppose the existence of a Jurassic lake of even the smaller or more moderate dimensions assigned by him. While I do not wish to be understood as denying the possibility of the existence of a great lake in Jurassic times extending as Dr. White has suggested from the Arkansas River in Colorado to the Black Hills of South Dakota, it does appear to me that our present knowledge of the character of the faunas, both terrestrial and aquatic (fresh-water) as well as of the lithogic and stratigraphic features exhibited by the beds themselves is decidedly against such a presumption. If I properly understand Dr. White he finds nothing in the character of the aquatic mollusca to preclude the possibility of their having lived and developed in smaller lakes. After a personal examination of the localities at Green River, Utah, at Grand River in western Colorado, Canyon City and Morrison in eastern Colorado, Como and Sheep Creek in southern Wyoming, at the Spanish Mines in eastern Wyoming, along the Big Horn Mountains in central Wyoming, about the Black Hills in South Dakota and in the country near Billings in southern Montana, in all of which localities the *Atlantosaurus beds* are exposed and exhibit in more or less abundance, the remains of those dinosaurs which are characteristic of them, I am convinced that neither the character of the vertebrate fauna nor the facts of stratigraphy at any one of these places can be taken as affording anything like conclusive evidence of the presence of a great body of water. At several of these localities, however, the occurrence at intervals of sandstones showing frequent examples of cross-bedding, ripple marks and even occasionally exhibiting footprints is conclusive proof that such sandstones had not their origin in the midst of a great lake, while the presence almost everywhere of the remains of terrestrial reptiles and less frequently of mammals tells only too plainly of an adjacent land-mass. In all this region I know of no locality where any considerable extent of the Atlantosaurus beds occurs, in which remains of quadrupedal, terrestrial dinosaurs have not been found. To my mind, this fact alone affords very strong presumptive evidence that in Jurassic times this entire region was the habitat of these dinosaurs, which it could not have been had it been covered by a great lake, for the structure of their limbs shows conclusively that the Dinosauria were not aquatic. Nor can I conceive of the possibility of the carcasses of terrestrial animals being carried out into the midst of so great a lake as that presupposed above and left in such abundance as the numbers of their bones in these deposits would indicate. An hypothesis, which it appears to me is far more reasonable and more nearly in accordance with the facts as we now know them, is to consider this region as presenting in late Jurassic and early Creta-

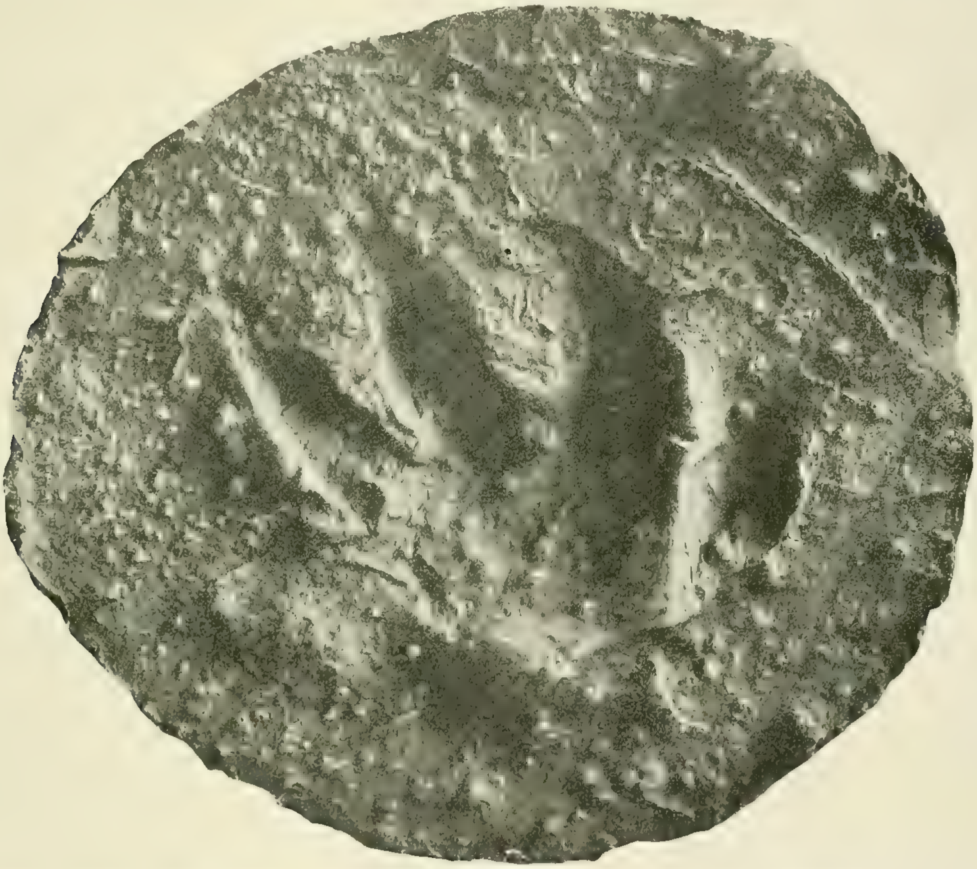


FIG. 23. Photograph of footprint in Jurassic sandstone, near Canyon City, Colorado.

ceous times the appearance of a low and comparatively level plain, with numerous lakes, both large and small, connected by an interlacing system of river channels. The whole, when covered over with luxuriant forests and broad savannas, made possible by the supposedly tropical climate of those times, would form an ideal habitat not alone for the large Dinosauria, but for the smaller reptiles and diminutive mammals of those days and for the fishes, mollusca and other aquatic life as well.

In Figs. 23 and 24 respectively, are reproductions of photographs of a footprint from the dinosaur beds near Canyon City, Colorado, and ripple marks from the same deposits along the base of the Big Horn Mountains in Wyoming.

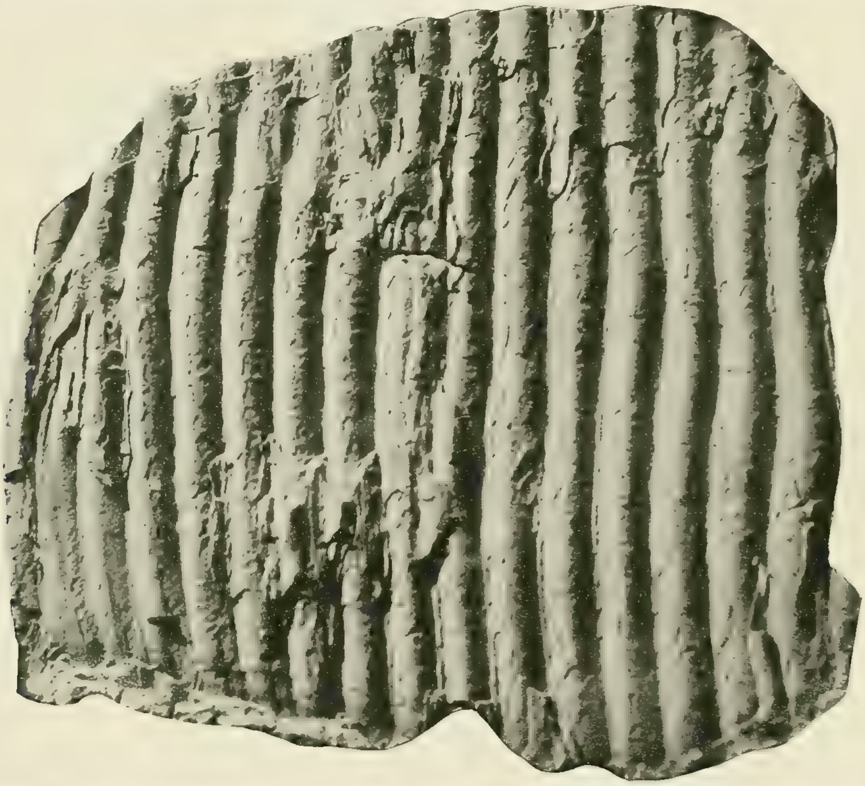


Fig. 24. Photograph of ripple marks on surface of Jurassic sandstone, Big Horn Mountains, Wyoming.

In Fig. 25 there is given the reproduction of a photograph by Dr. E. H. Barbour of the locality near Canyon City, Colorado, where were located the quarries so long worked by Professors Marsh and Cope. The dark area in the middle foreground just back of the tent is the quarry so long and successfully worked by Professor Marsh and recently worked with equal success by Mr. Utterback for the Carnegie Museum. At *A* directly across the cañon and on about the same horizon was located another quarry also worked with some success by Marsh. At *B* a little above and on the same side of the small cañon, but in a slightly different horizon, in a layer of arenaceous shales there occurs a bed of Unios from which were obtained most of the species described by Dr. C. A. White as coming from this locality, while the shales underlying the thick stratum of sandstone seen at the top of the escarpment forming the cañon wall just to the left and in front of the tent contains numerous small lenses of impure limestone filled with the silicified remains of fresh-water gasteropods and the stems and seeds of small aquatic plants apparently pertaining to some species of Chara. These limestone lenses are especially abundant and quite fossiliferous at the locality marked *C* in the photograph and at a point on the same horizon of this talus-covered slope a few rods in front of the extreme foreground of the photograph and therefore not shown in the picture. The line of trees just above and in front of the Marsh quarry marks the crest of the narrow ridge that at this point separates the dry cañon in the middle of the picture from Oil Creek on the extreme left. At this point this ridge is about 100 yards in width from the brink of the cliff overlooking the bed of the creek and that of the dry cañon. In the wall facing Oil Creek at the same horizon at which the bones occur in such abundance at the adjacent quarry, dinosaur bones may be seen imbedded in similar sandstones, showing that the bone-bearing horizon extends quite through the ridge. From the great abundance in which the bones were found up to the limits of the quarry as last worked and as shown in the accompanying diagrams, it is only reasonable to suppose that many rare treasures await the explorer who has the courage and funds necessary to remove the 15 to 40 feet of sandstones and shales beneath which they now lie buried.

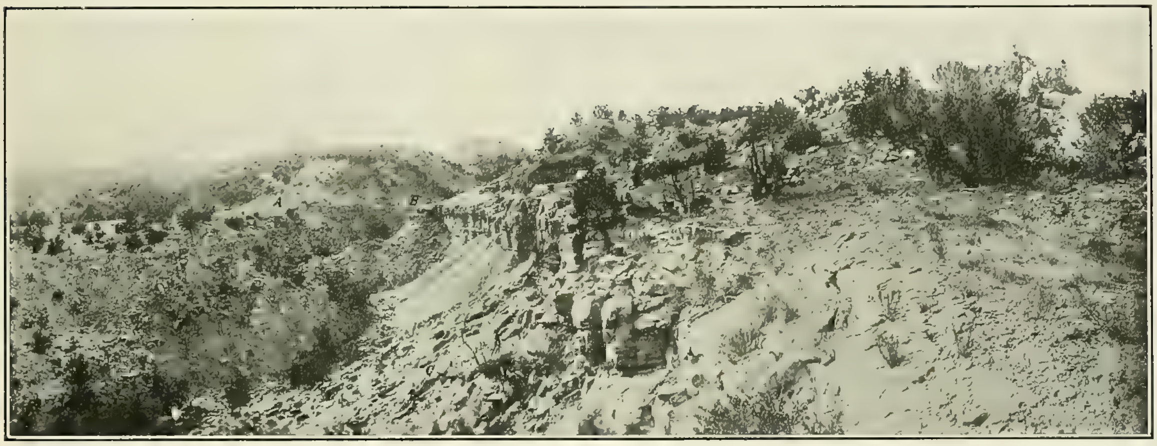


FIG. 25. View of *Atlantosaurus beds* at entrance to Garden Park, eight miles northeast of Canyon City, Colorado. From a photograph by Dr. E. H. Barbour.

The isolated butte known as "Cottage Rock" seen at the head of the dry cañon in the middle background is capped with some fifty to one hundred feet of light-colored, massive sandstones generally referred to as Dakota, although neither here nor elsewhere in this region in so far as I am aware, are these sandstones clearly distinguishable from the Jurassic. Cottage Rock is situated about three quarters of a mile north of the Marsh quarry and the top of the uppermost shales in this butte which are clearly recognizable as pertaining to the *Atlantosaurus beds* is estimated to be from 300 to 350 feet above the bone-bearing horizon at the Marsh quarry.

The isolated conical butte shown in Fig. 26, and locally known as the "Nipple" is situated some 300 yards back and a little to the right of "Cottage Rock." It stands on the edge of the escarpment overlooking the valley of "Garden Park" through which flows Oil Creek. This Tepee butte is composed almost entirely of shales pertaining to the uppermost *Atlantosaurus beds.* It is capped with a mere remnant of a former sandstone ledge belonging either to the top of the *Atlantosaurus beds* or the base of the *Dakota.* About the base and over the slopes of this butte fragmentary dinosaurian remains occur in considerable abundance and the locality was worked to a considerable extent by Professor Cope. One of his abandoned trenches may be seen on the left at the foot of the butte in the photograph.

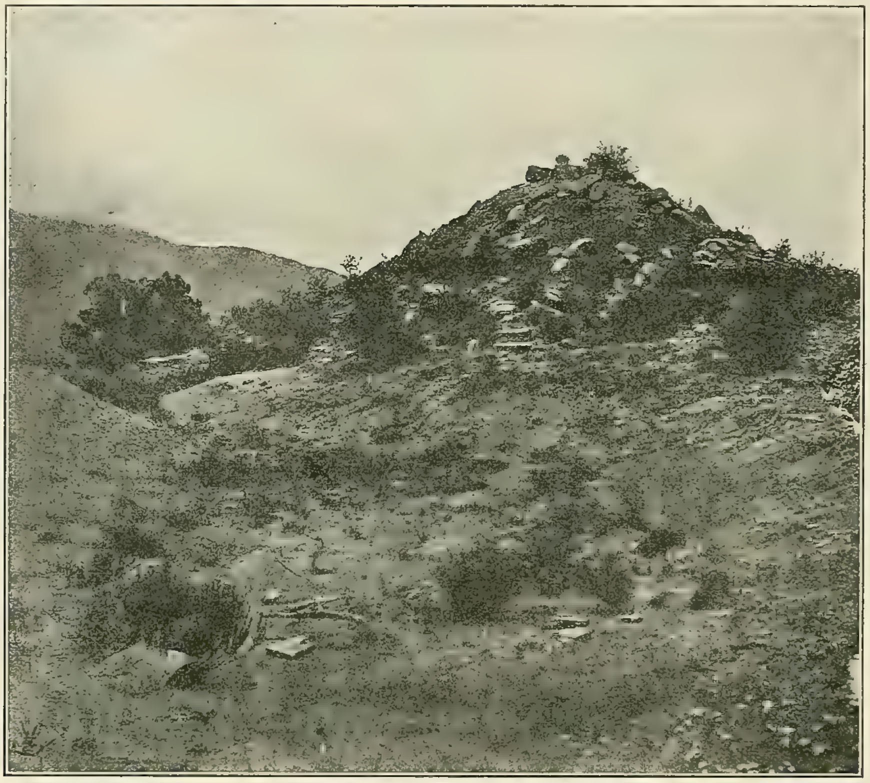


Fig. 26. The "Nipple" from the north, showing in the foreground the trench cut by Professor Cope in collecting Dinosaur remains.

Another quarry long worked by Professor Cope is shown in Fig. 27. This quarry is situated about 500 yards west of the "Nipple" and the dinosaur bones, belonging for the most part to *Camarasaurus*, were found imbedded in a thick stratum of chocolate-colored shales immediately beneath the light-colored, heavily bedded, jointed sandstones seen at the summit in the figure and provisionally referred to the Dakota. Between this quarry and the "Nipple" there lies a comparatively level plain some 500 yards in width covered over with a growth of juniper, piñon and other bushes characteristic of this region as shown in Fig. 28.

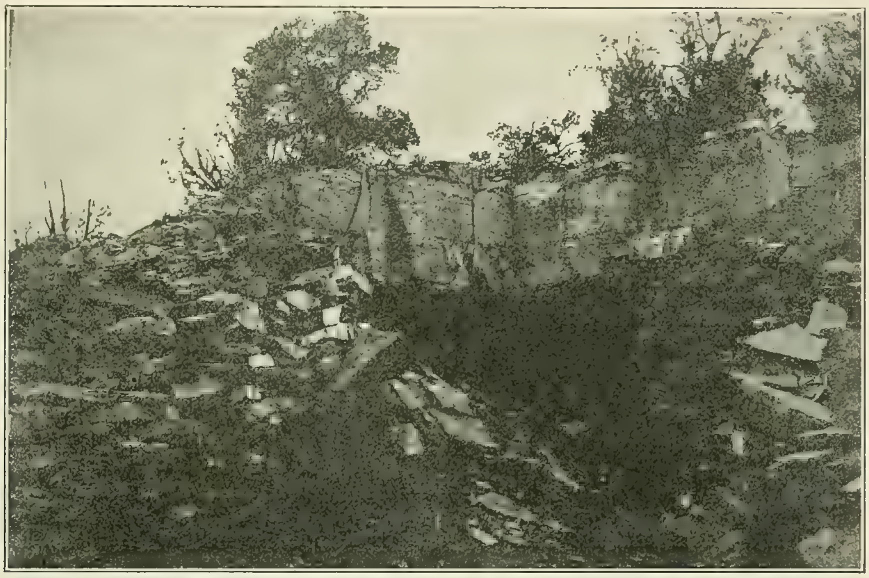


FIG. 27. Eastern entrance to Cope quarry. Light-colored Dakota sandstone at top underlaid by chocolate-colored shales with remains of Camarasaurus.

That quarry in this region which was perhaps worked with most success by Professor Cope or men in his employ was situated about one mile north of that last mentioned and at the same horizon, in chocolate-colored shales lying just beneath the supposed Dakota sandstones. This last quarry I have never visited, but Mr. Lucas, who was Professor Cope's principal collector in this region, accompanied Mr. Utterback to the quarry and explained to him how the bones were found. According to Mr. Lucas the more complete of the two skeletons of *Camarasaurus supremus* which are now known to have been treated as one skeleton in Cope's descriptions of the species, was found at this last locality. The location of this quarry is about one mile north of the "Nipple" and on the edge of the escarpment facing Garden Park.

The above are the most important localities that have been worked for fossils in this region although dinosaur remains have been found here at many other places but in no considerable abundance. It will be noticed from the above remarks regarding the location of the several quarries worked in this region by Professors Marsh and Cope, that the quarries operated by Marsh were in a distinctly lower horizon than those from which Cope secured his material. While Professor Cope's material all came from near the summit of the *Atlantosaurus beds*, that of Professor Marsh was derived from the lower members of those beds, certainly not more than 100 to 150 feet above the Red Sandstones. This difference in horizon, which can be represented by scarcely less than 300 to 350 feet of sandstones and shales, must of necessity represent an enormous time interval, much greater perhaps than is ordinarily represented by sedimentary deposits of an equal thickness, for from the manner in which the sandstones and shales replace one another both laterally and vertically, and from the frequent examples of cross-bedding and ripple-marked surfaces exhibited by the sandstones it is evident that the region was not one of continuous and universal deposition, but that degradation and aggradation were in simultaneous operation and that while on the whole the latter agency predominated there may have been and doubtless were considerable intervals during which erosive agencies were the more efficient of the two. As should be expected the enormous time interval which elapsed between the deposition of the sandstones of the Marsh quarry and the shales of the Cope quarries, some 350 feet higher, was sufficient to

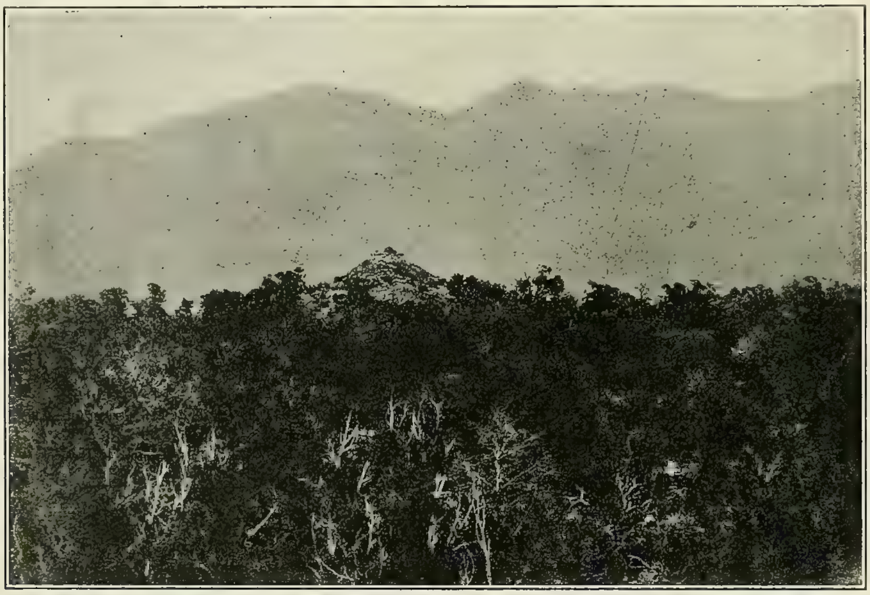


Fig. 28. View from near Cope quarry with the "Nipple" in the middle foreground and Cooper Mountain in the distance. Garden Park lies in a depression about 600 feet below the "Nipple" between the crest of the bluff, indicated by the line of trees on either side of the "Nipple," and Cooper Mountain.

accomplish considerable changes in the dinosaurian fauna of this region, and these changes are readily apparent in the faunas from these two horizons, though for obvious reasons the present paper is not the place in which to discuss them. They will no doubt be fully recognized and discussed by Professor H. F. Osborn in his Monograph on the Sauropoda now in course of preparation for the United States Geological Survey.

Synonymy of the Atlantosaurus Beds.

Although these beds were first recognized, named and adequately described both lithologically and faunally, by Professor Marsh they have received several different appellations by subsequent authors. Scott has called them the *Como-beds;* by Cross they were referred to as the *Morrison beds;* Jenney named them the *Beulah Shales* and this name was used by Darton. Considering the usual similarity of the faunal and lithologic features of these beds wherever they are known to exist and the ease with which they may be recognized even at different and widely separated localities, it would seem somewhat unfortunate that they have received so many names.

Since Marsh's term the *Atlantosaurus beds* has priority, and has become well known through long and general usage there would seem no good reason why it should not be retained. Even should the reptilian genus *Atlantosaurus,* as contended by some but which has yet to be demonstrated, prove to be a synonym and have to be abandoned, this would not invalidate the name of the formation. It would be quite as reasonable to maintain that since Fort Union on the Missouri River from which the *Fort Union beds* took their name, is no longer in existence that this great formation should receive a new name. While the present writer is entirely in favor of basing all new formation names on geographic names taken from the localities where such formations are first studied or are best represented, it does not appear desirable to make this rule retrogressive. Such retrogressive application of this rule would not only work an injustice to many pioneers in American geology, but what is of even greater importance, it would result in augmenting still further that confusion which already exists in our geologic formation names. Surely from that standpoint alone there is sufficient reason for deprecating any attempt to duplicate such names. Nor does the plea advanced by some who have been most active in giving new names to old and well known formations, that it is easier to give a new name than to turn bibliographer and trace out the synonymy and priority of the names already given by others, give promise of being justified by the results which are sure to follow such a course. To the present writer it would appear much the better plan to accept formation names for formations already known, as we find them having due respect for priority and general usage; to adopt as a general rule for our guidance in the conferring of new names on new formations the theory that each such name should be derived from the name of some locality at which the formation is well displayed and may be easily recognized and studied. It might also be well to remember in this connection that we are no more competent to legislate for future generations than were our forefathers.

Age of the Atlantosaurus Beds.

There has been considerable difference of opinion regarding the age of the *Atlantosaurus Beds*. By some they have been regarded as of Lower Cretaceous age and by others as Upper Jurassic. When first discovered, these beds were referred by Professor Marsh to the Cretaceous (see *American Journal of Science*, July, 1877, pp. 87–88). In December of this same year Professor Marsh referred these same deposits to the Upper Jurassic and in a note describing a new fish, *Ceratodus güntheri*, from these deposits, published in the January number of the *American Journal of Science* for 1878 he named them the *Atlantosaurus beds*. He ever after consistently maintained their Upper Jurassic age. Cope and Hayden on the other hand referred these beds, more especially as developed at Canyon City, Colorado, and at Morrison to the *Dakota*, now generally recognized as pertaining to the lowermost member of the Upper Cretaceous. The following paragraph from page 234 of the Proceedings of the American Philosophical Society was written by Professor Cope and it is significant in this connection. It is as follows: "Dr. Hayden visited the locality of Mr. Lucas' excavations (near Canyon City) and informs me that the formation from which the *Camarasaurus* was obtained is the Dakota. Professor Marsh has attempted to identify what is, according to Professor Mudge, the same horizon, one hundred miles north of Canyon City with the Wealden of England. Specimens from the northern locality which I have examined render it certain that the horizon is that of Mr. Lucas' excavations. Of this I may say that there is no paleontological evidence of its identity with the Wealden. The resemblance of the vertebrate fossils to those of the English Oölite is much greater, but not sufficient as yet for identification." Ten years later however (*American Naturalist*, May, 1887, pp. 446–447) Cope placed these beds in the Jurassic to which they had been previously referred by both Marsh and King and which, from the paragraph quoted above, would seem to have been the only course open to him. Indeed there is little doubt that when Cope first referred these beds to the Dakota he did so entirely upon the determinations of Dr. Hayden and regardless of the paleontological evidences afforded by the fauna they contained, which, such as it was, as is shown by the quotation above, he regarded as pointing to a decidedly greater antiquity even than the

Wealden, with which Marsh had been in favor of correlating them and which was at that time very generally regarded as of Upper Jurassic age though at present considered by most geologists as representing the lowermost member of the Cretaceous.

Professor Lester F. Ward, on page 377 of Part II. of the Twentieth Annual Report of the United States Geological Survey, in commencing his treatise on the Jurassic cycads dismisses the age of these beds as developed in Wyoming with the remark that there is no doubt as to their being Jurassic, and on page 384 he says of the cycads from the Freeze Out Hills locality that "in some respects they resemble the specimens from the Purbeck beds of the Isle of Portland."

Professor Wilber C. Knight[10] has remarked as follows concerning the age of the *Atlantosaurus* (*Como*) *beds*. "There can be no mistake in assigning the Como stage to the Upper Jurassic, but it seems quite possible that it is more closely allied to the Purbeckian than to the Oxfordian."

Darton[11] is not very clear as to just what age he wishes to refer these beds. In his diagram at the top of page 387 of the paper just cited he refers them to the "Lower Cretaceous (or Jurassic)?" and immediately after on the same page in his table of the thickness of formations, and again on page 393 in describing the character and distribution of the *Atlantosaurus beds* (*Beulah Shales*) he refers them to the Jurassic without a query. It would seem therefore that he also favored their Jurassic age.

Osborn has I think consistently maintained the Jurassic age of these deposits. On the other hand Scott and Williston have been in favor of placing them in the Lower Cretaceous.

As already noticed Dr. C. A. White has regarded these beds as of Jurassic age though apparently relying entirely upon the evidence afforded by the vertebrates and remarking that the fresh-water invertebrates of the same beds are so modern in type as of themselves to offer no suggestion of a greater age than Tertiary. And again he adds: "Indeed so modern is the facies . . . that one is surprised to find only a single type among them which is not common among American living fresh-water species."

In discussing the age of any geological horizon which is fossiliferous two classes of evidence are of especial importance. First in importance is its stratigraphic position and second the nature of its included fossils, vertebrates, invertebrates and plants. The relative value of the different classes of fossils for purposes of correlation vary according as the beds in question are of marine or fresh-water origin. While marine invertebrates and most terrestrial and aquatic vertebrates are as a rule safe guides for purposes of correlation and second only in value to direct stratigraphic evidence, fresh-water invertebrates, plants and certain vertebrates as for instance turtles, crocodiles and some fishes are as a rule much less reliable guides.

---

[10] *Bull. Geol. Soc. Am.*, Vol. 11, p. 387.

[11] *Bull. Geol. Soc. Am.*, Vol. 10, pp. 387, 393.

Stratigraphic Position of the Atlantosaurus Beds.—As originally applied the term *Atlantosaurus beds* refers to that series of sandstones and shales, some 450 feet in thickness and containing the remains of dinosaurs, small mammals, etc., lying between the red Triassic? sandstones below and the Dakota sandstones above on either side of the cañon of Four Mile Creek (Oil Creek) near Canyon City, Colorado. The dinosaur remains upon which Professor Marsh relied for the determination of the age of these deposits at this locality all came from the lowermost 150 feet of the series and it may therefore eventually prove advisable to limit the use of the term to the lower one third of the series. Farther north in Wyoming and about the Black Hills in South Dakota similar dinosaur beds are separated from the Red Beds by a series of marine shales and limestones named by Marsh the *Baptanodon beds.* These latter beds are rich in the remains of marine vertebrates and invertebrates and are universally regarded as of Middle or Upper Jurassic age, while the overlying dinosaur beds have as universally been referred to the *Atlantosaurus beds* usually considered, as noted above, as of Upper Jurassic age. The marine *Baptanodon beds* throughout Wyoming and South Dakota are everywhere found accompanying and underlying the fresh-water *Atlantosaurus beds* though thinning out toward the south and entirely disappearing as we approach the Wyoming and Colorado state line. As already noticed they are entirely absent in the locality near Canyon City, Colorado, the *Atlantosaurus beds* there resting directly upon the *Red beds* and with at least apparent conformity. Nor does there appear to be any material break in the conditions of sedimentation in this region from the base of the *Atlantosaurus beds* to the summit of the *Dakota.* If this be true it would appear that at Canyon City the lower members of the *Atlantosaurus beds*, those worked by Marsh and by Mr. Utterback, are the fresh-water equivalents of the marine *Baptanodon beds* farther north, while the upper beds or those worked by Cope would become the equivalents of the *Atlantosaurus beds* at Morrison, Colorado, and at various localities in Wyoming and South Dakota. Such evidences of stratigraphy as there are prove conclusively that the *Atlantosaurus beds* at Canyon City overlie the Triassic and underlie the Dakota and that they are intermediate in age between the two and are therefore of either Jurassic or Lower Cretaceous age or that they represent, either wholly or in part, both those horizons. The latter seems to me the more reasonable conclusion when considered from the standpoint of stratigraphy alone.

Evidences as to Age Afforded by the Fauna and Flora.—As already noticed Professor Ward has regarded the cycads from the *Atlantosaurus beds* of the Freeze Out Hills, Wyoming, locality as indicative of a Jurassic age.

Invertebrate paleontologists have I think been unanimous in referring the marine *Baptanodon beds* to the Middle and Upper Jura. They have it appears been most frequently correlated with the Oxfordian or lower member of the Middle Oölite. By some however they have been placed in the Lower Oolite. Since, as has been shown above, there is not a little evidence in favor of considering the lowermost 150 feet of the *Atlantosaurus beds* at Canyon City as the equivalents of these marine beds in the north the age of the latter, as determined by its marine invertebrates, may be taken as having a certain bearing on that of the former series. The vertebrates of these marine beds appear to point to a somewhat greater antiquity than the invertebrates, for *Baptanodon,* the most abundant and best known form, has its nearest ally in the Liassic *Ophthalmosaurus* of Europe, and Mr. C. W. Gilmore, who is engaged in a thorough and exhaustive study of the American forms, has recently shown that the American form was not edentulous as had been supposed and that it is scarcely distinguishable, at least generically, from the European Liassic genus *Ophthalmosaurus.*

Turning now to the fauna of the *Atlantosaurus beds,* it is readily apparent that the dinosaurs offer the best, indeed almost the only reliable paleontological evidence as to their age. We have already called attention to the fact that Cope regarded the dinosaurs of the uppermost of these beds as being most like those of the English Oölite and we have shown that *Haplocanthosaurus* from the lower half of the series resembles most closely *Cetiosaurus* from the Great Oölite near Oxford.

Marsh was wont to correlate the *Atlantosaurus beds* with the Wealden which he regarded as of Upper Jurassic age. On just what evidence he relied for this correlation is not quite clear. Nor does a comparison of the dinosaurian faunas of these two horizons seem to me to warrant such correlation. While from the fragmentary nature of much of the material upon which the different genera and species are based it is clearly impossible to make satisfactory comparisons in many instances between the more closely related genera and species of American and European dinosaurs, nevertheless when comparisons of the faunas as a whole are instituted between the various American and European horizons most striking and important resemblances and dissimilarities are at once apparent. Thus while in the *Atlantosaurus beds* the Sauropoda are the predominant forms both as regards size and the number of genera, species and individuals in the Wealden they are almost entirely replaced by the Predentata and Theropoda. And the Iguanodontia so abundant in the latter formation are quite unknown in the former. The same dissimilarity though in a less striking degree is noticeable when the fauna of the *Purbeck* is compared with that of the *Atlantosaurus beds*, and it is not until we get down into the middle of the Oölite that we find a dinosaurian fuana comparable even with that of the upper and middle *Atlantosaurus beds.*

In consideration of the evidences mentioned above it appears to the present writer that the dinosaurian fauna of the *Atlantosaurus beds*, as we now know it is unmistakably Jurassic in type, but that these beds may in their uppermost members represent a portion at least of the lower Cretaceous.

CARNEGIE MUSEUM, April 15, 1903.

ADDITIONAL REMARKS ON DIPLODOCUS.

By J. B. HATCHER.

Since publishing my memoir[1] on the osteology of *Diplodocus* additional discoveries have thrown more light on the structure of these strange reptiles. It thus becomes necessary to make certain alterations in the description and restoration then given, especially relating to the structure of the fore limbs and feet. As stated in the text of my memoir there were at that time in the collections of this museum no representatives of the fore limbs or feet of *Diplodocus* and the brief descriptions of those elements there given was based entirely upon the published descriptions by Professor Osborn and upon photographs of the limbs kindly loaned by him. Fortunate discoveries of the fore limbs and feet of *Brontosaurus* (No. 563) by Mr. C. W. Gilmore and of the greater portion of a skeleton of *Diplodocus* (No. 662) by Mr. W. H. Utterback have demonstrated two important errors in my previous paper. These are:

First.—The radial articulation at the distal end of the humerus is on the internal side and anterior to the internal portion of the ulnar articulation instead of being external and anterior to the latter as stated in my memoir. When in position the proximal end of the ulna entirely enclosed that of the radius posteriorly and externally, as shown in Fig. 1, and its articular surface is opposed to that of the distal end of the humerus posteriorly throughout its entire breadth and presents a broad and deep anterior projection enclosing the radius externally and articulating with the anterior and external surface of the distal end of the humerus.

---

[1] *Memoirs Carnegie Museum*, Vol. I., No. 1, pp. 1–63, Pl. 1–13.

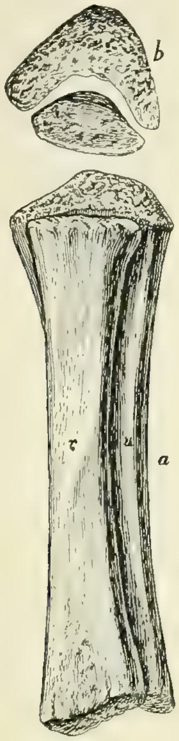


FIG. 1.

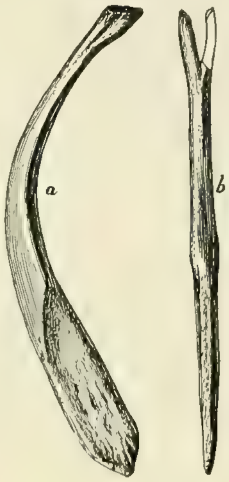


FIG. 2.

FIG. 1. *a*, front view of radius and ulna of *Diplodocus* (No. 662). *b*, proximal end of same. Both figures are one tenth natural size and show bones as seen when in position.

FIG. 2. *a*, front view of supposed clavicle of *Diplodocus*. *b*, internal view of same (No. 662), one tenth natural size.

The contact of the radius with the humerus is thus limited to the antero-internal surface instead of the antero-external as erroneously shown in my original restoration of the skeleton. The radius and ulna do not cross each other so completely as supposed by Osborn and Granger, but occupied the position relative to one another shown in Fig. 1.

Second.—The structure of the manus was entaxonic instead of mesaxonic as erroneously represented in my original restoration where, as stated in the text, I followed Osborn, having at that time no material upon which to base a restoration of those elements. The manus was doubtless somewhat more plantigrade than I at that time represented it. In the present restoration these errors in the structure of the fore limbs and manus have been corrected. The principal characters of the latter are taken from the manus of *Brontosaurus*, a detailed account of the structure of which was recently published by the writer.[2]

The Supposed Clavicles. — In my original description of *Diplodocus carnegii* I figured and described a peculiar bone which I then considered as a clavicle, though at the same time expressing some doubt as to its real nature. Fortunately we have found associated with another skeleton (No. 662) of *Diplodocus* a second and more complete clavicle? shown here in Fig. 2, *a*, *b*. The present specimen is somewhat incomplete at the bifid extremity, the smaller branch having been broken away, the opposite end is complete, somewhat expanded and spatulate as shown in the figures. The spatulate portion has a length of 265 millimeters, a maximum breadth of 75 millimeters and an average thickness of about 24 millimeters.

The entire length of the bone measuring along the arc of that portion of the circle which it describes is 620 millimeters. Between the expanded portion and the forked extremity the bone is irregularly elliptical or subcircular in cross-section.

This bone is asymmetrical and is to all appearances a paired bone. In neither instance have we as yet secured its opposite, though this is still possible with that one now being considered, a considerable portion of the skeleton still remaining to be unearthed. Just at the point where the rounded shaft passes into the flattened, spatulate extremity there is on one side a shallow groove running obliquely across the surface of the bone. This groove has the appearance of having been formed by the overlapping edge of a coracoid or sternal. The flattened spatulate extremity presents a slightly rugose, fibrous surface as though it had been imbedded in cartilaginous or muscular tissue, and this together with the bifid nature of the other extremity has suggested the possibility that the bone might be an os penis; in which case the bifid extremity would be the distal end and the flattened the proximal extremity. Against the probability of this assumption however, the marked asymmetry of the bone offers a potent argument and I am still strongly inclined to consider it a clavicle as which it might very readily have functioned. Although clavicles have not heretofore been recognized in the Dinosauria there would seem no good reason for supposing that they were not present in some members of that group. A clavicle of the size and form of the element under discussion, if attached to the anterior edge of the broadly expanded sternals, coracoid and prescapula, could not have failed in giving additional strength and rigidity to this portion of the skeleton.

The Anterior Cervicals. — In my former paper, owing to the incomplete nature of cervicals 3, 4, 5, they were figured as without cervical ribs; later discoveries (No. 662) demonstrate that ribs were present on all these vertebræ and they are so shown in the accompanying restoration (Plate F).

---

[2] See *Science*, N. S., Vol. XIV., pp. 1015–1047; and *Annals Carnegie Museum*, Vol. I., pp. 356–376.

The cervical vertebra figured by Marsh and reproduced as text Fig. 24 in my memoir on *Diplodocus*, although referred by Marsh to *Diplodocus longus*, is now known to have pertained to a species of *Brontosaurus* instead, and hence is of no value in distinguishing the different species of *Diplodocus* as I then supposed.

PLATE I. Presacral vertebræ of type (No. 572) of *Haplocanthosaurus priscus*, one tenth natural size. Series 1, as seen from right side; Series 2, as seen from in front; Series 3, as seen from behind. *C* 14 and *C* 15, cervicals 14 and 15; 1, first dorsal; 6–14, dorsals six to fourteen respectively; *pzl*, postzygapophysial lamina; *ol*, oblique lamina; *hl*, horizontal lamina; *dl*, diapophysial lamina; *azl*, prezygapophysial lamina; *S*, modified surface for muscular attachment of scapula; *t* or *tf*, tubercular rib facet; *c* or *cf*, capitular rib facet, *al*, inferior blade of diapophysial lamina in first dorsal and prespinal lamina in sixth dorsal.

PLATE II. Vertebræ of type (No. 879) of *Haplocanthosaurus utterbacki*, one tenth natural size. Series 1 and 2, dorsals; 3 and 4, cervicals; 5, anterior caudals.

PLATE III. Nineteen anterior caudal vertebræ of type (No. 572) of *Haplocanthosaurus priscus*, one tenth natural size. Series 1, seen from right side; 2, seen from in front; 3, from behind.

PLATE IV. 1. Pelvis of *Brontosaurus excelsus* (No. 563); 2. Pelvis of *Diplodocus carnegii* (No. 94); 3. Pelvis of *Haplocanthosaurus priscus* (No. 572). All one tenth natural size and seen from left side. *il.*, ilium; *p. p.*, pubic peduncle; *i. p.*, ischial peduncle; *g. c.*, acetabulum; *pb.*, pubis; *is.*, ischium; *a.*, anterior extremity; *p.*, posterior extremity; 1, 2, 3, 4, 5, spines of first, second, third, fourth and fifth sacrals.

PLATE V. 1. Inferior view of sacrum of *Haplocanthosaurus priscus* with ilia attached (No. 572). *a*, anterior end; *p*, posterior; *pp*, pubic peduncle; *is*, ischiac peduncle; *pf*, foramen between ilium and parapophyses of first sacral.

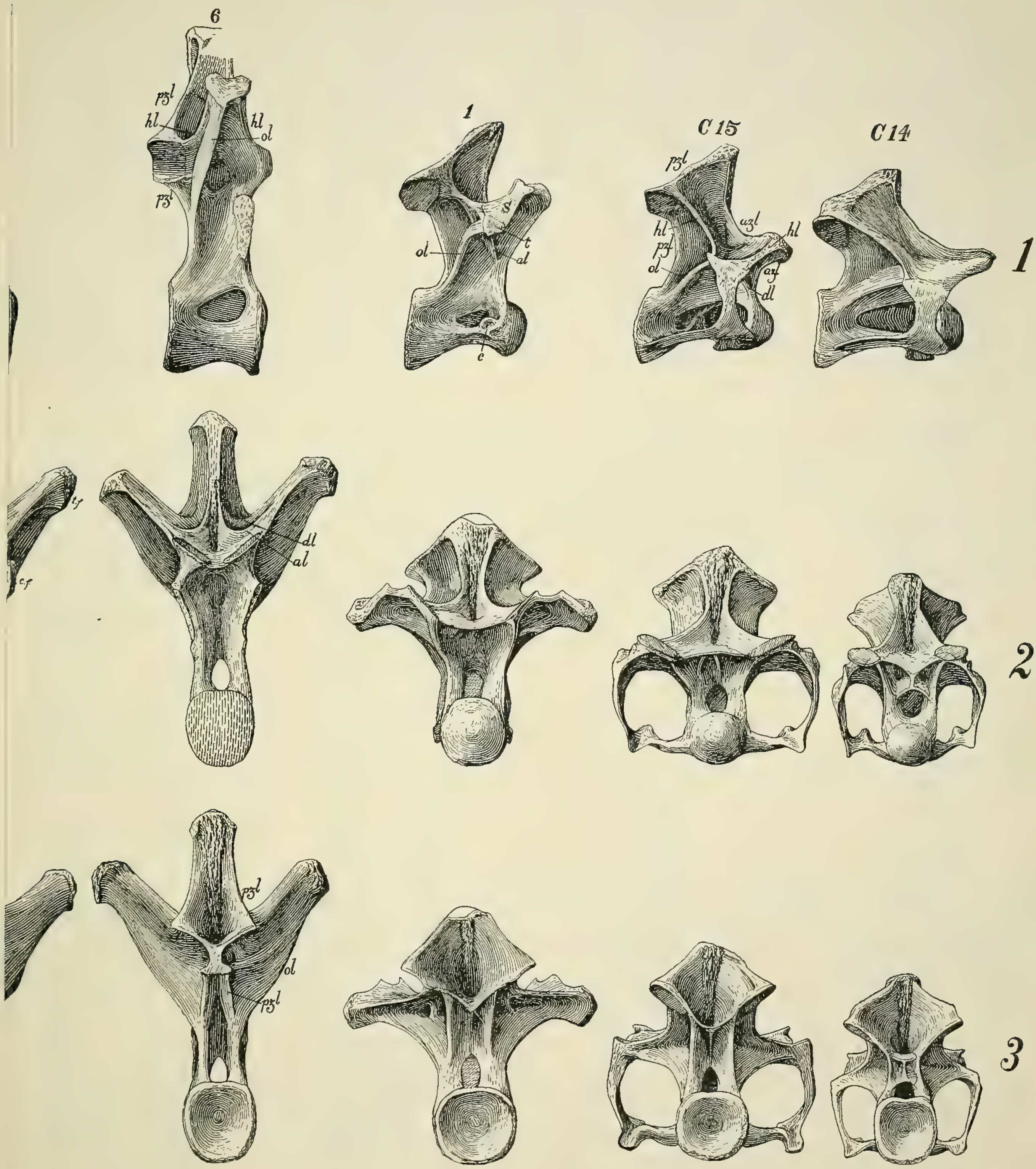
2. Anterior view of pelvis of same with ischia detached. *pp*, pubic peduncle; *p*, pubis; *ps*, pubic symphysis; *pt*, pubic foramen.

3. Posterior view of same, with pubis detached and anterior expanse of ilia not shown. *ip*, ischiac peduncle; *is*, ischium. All one tenth natural size.

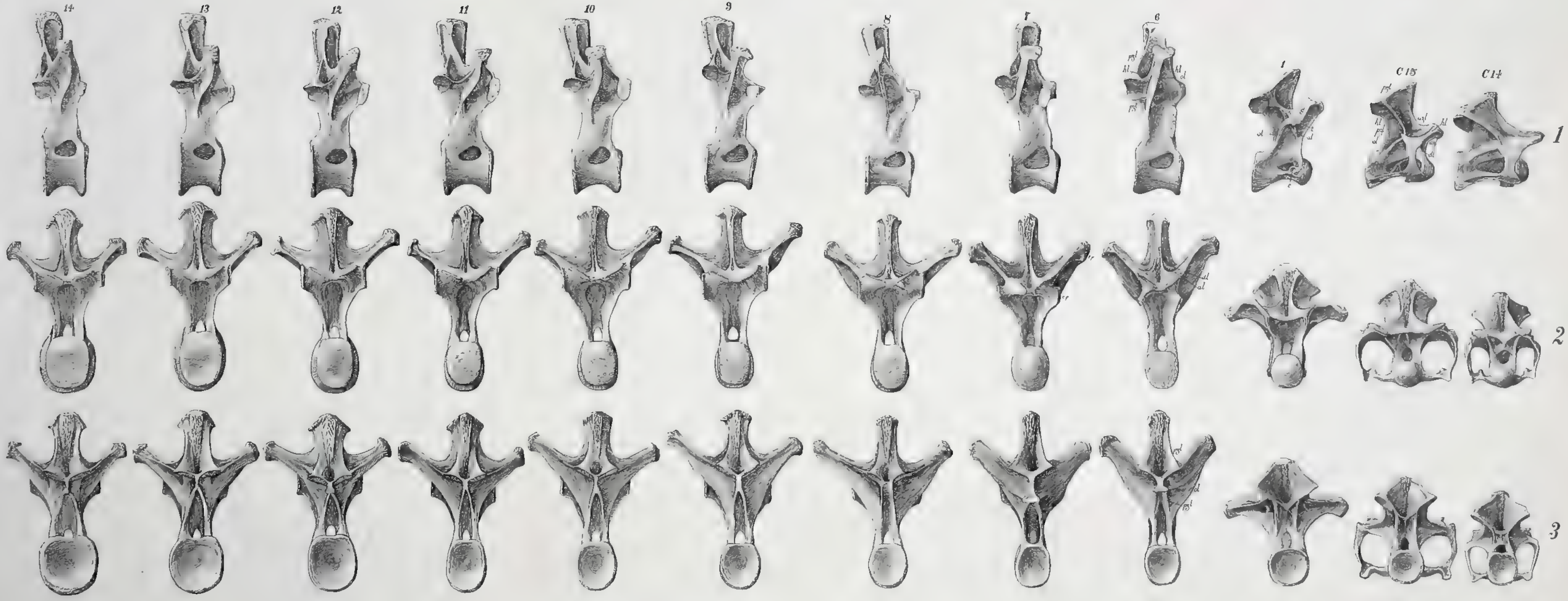
PLATE VI. Restoration of *Diplodocus carnegii* Hatcher.

From material in the collections of the Carnegie Museum, one thirtieth natural size.

PLATE I.

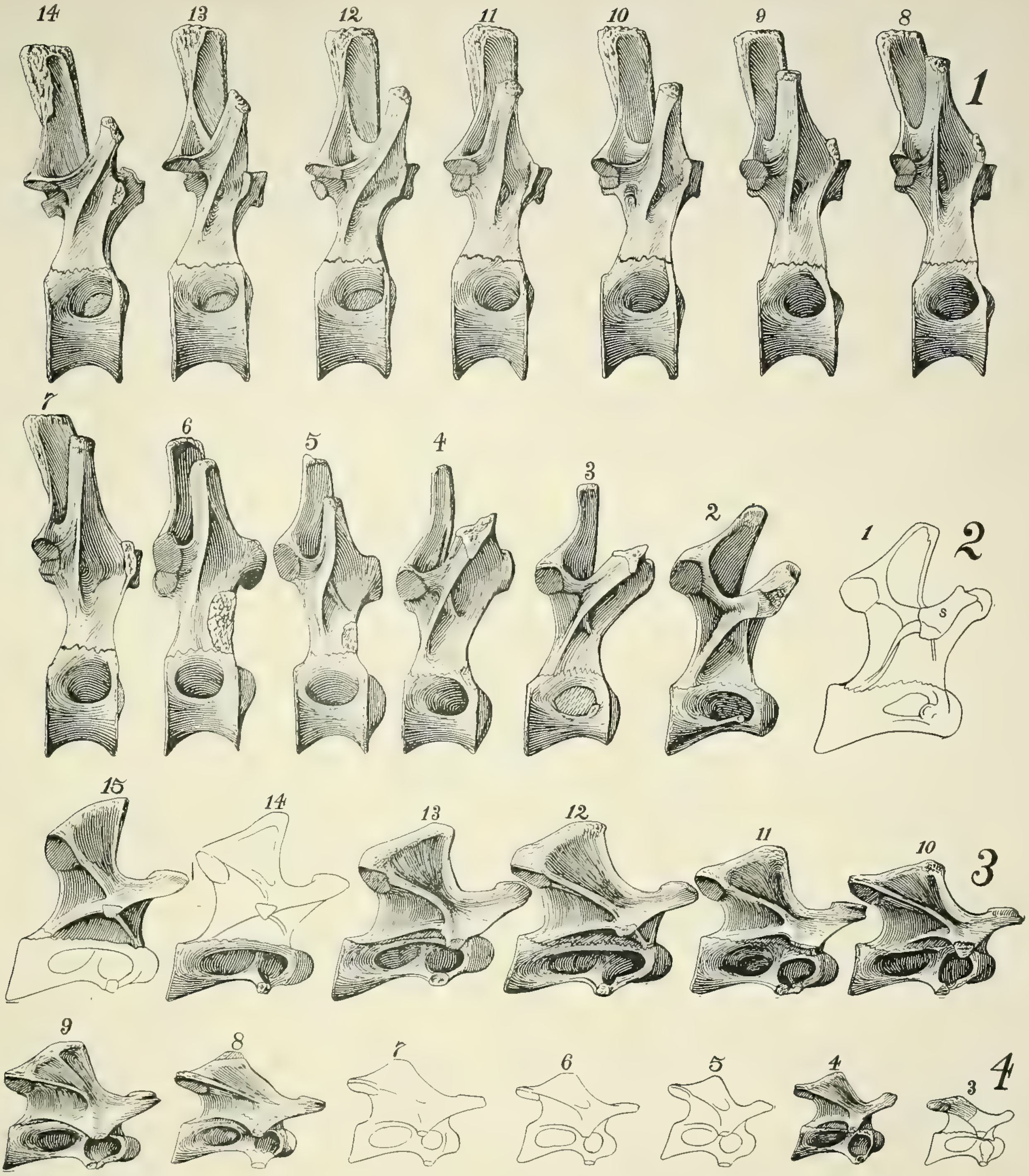


. SIZE. (No. 572.)



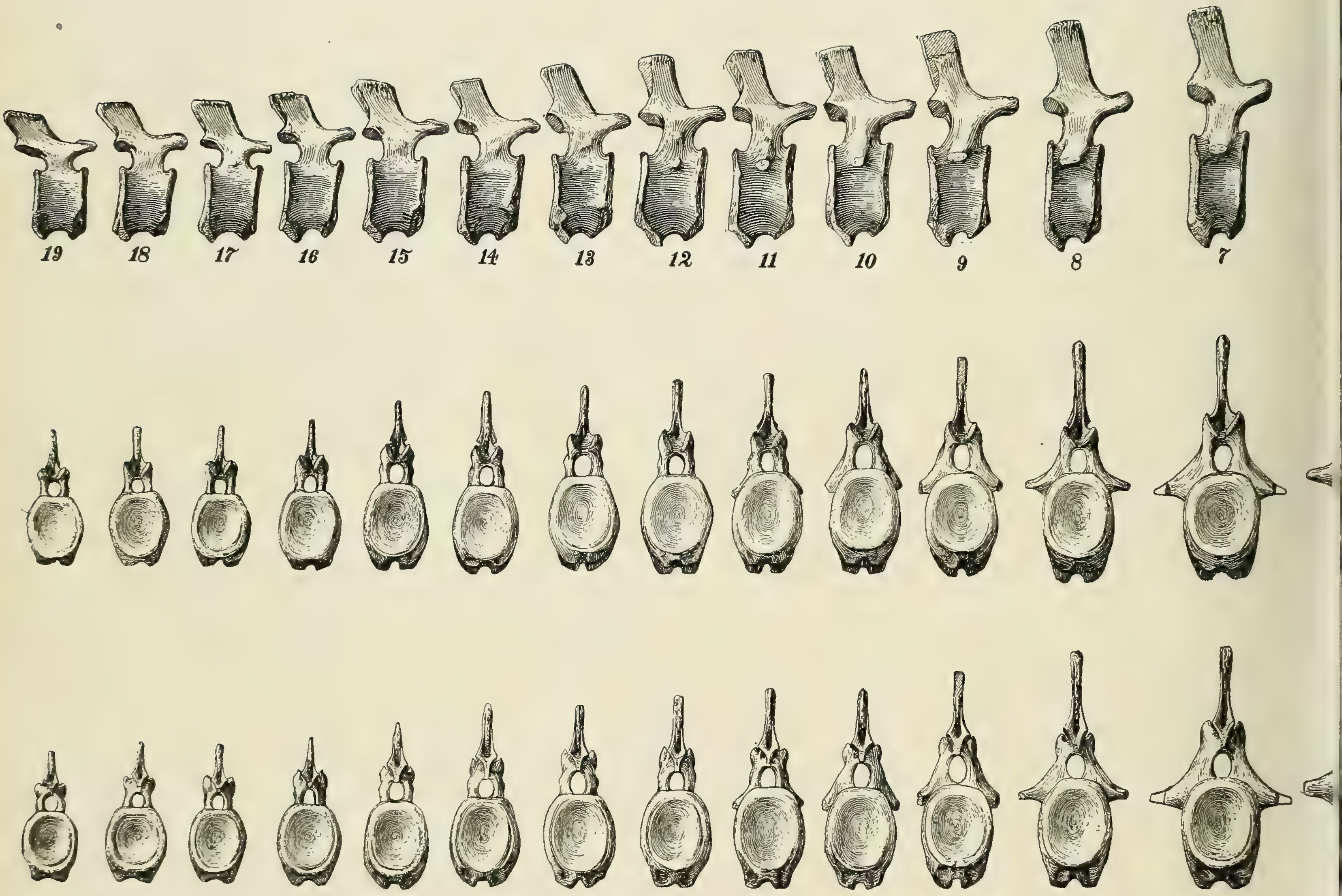
Sydney Prentice del.

Presacral Vertebræ of Type of *Haplacanthosaurus priscus.* 1, Side view; 2, Anterior view; 3, Posterior view. $\frac{1}{10}$ Nat. size. (No. 572.)



SYDNEY PRENTICE DEL.

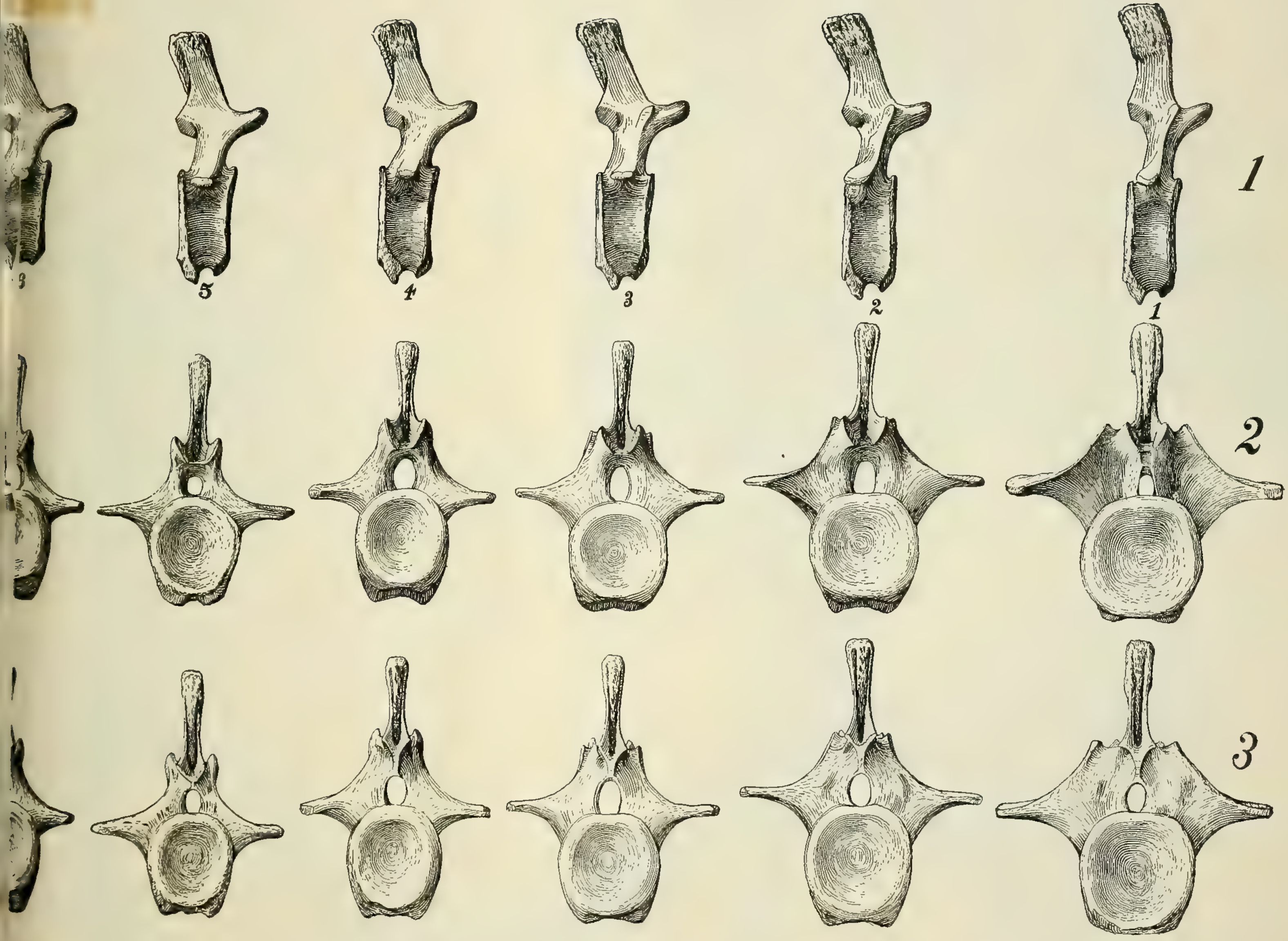
VERTEBRÆ OF TYPE OF *HAPLACANTHOSAURUS UTTERBACKII.* 1, 2, DORSALS; 3, 4, CERVICALS; 5, CAUDALS. $\frac{1}{10}$ NAT. SIZE. (No. 879.)



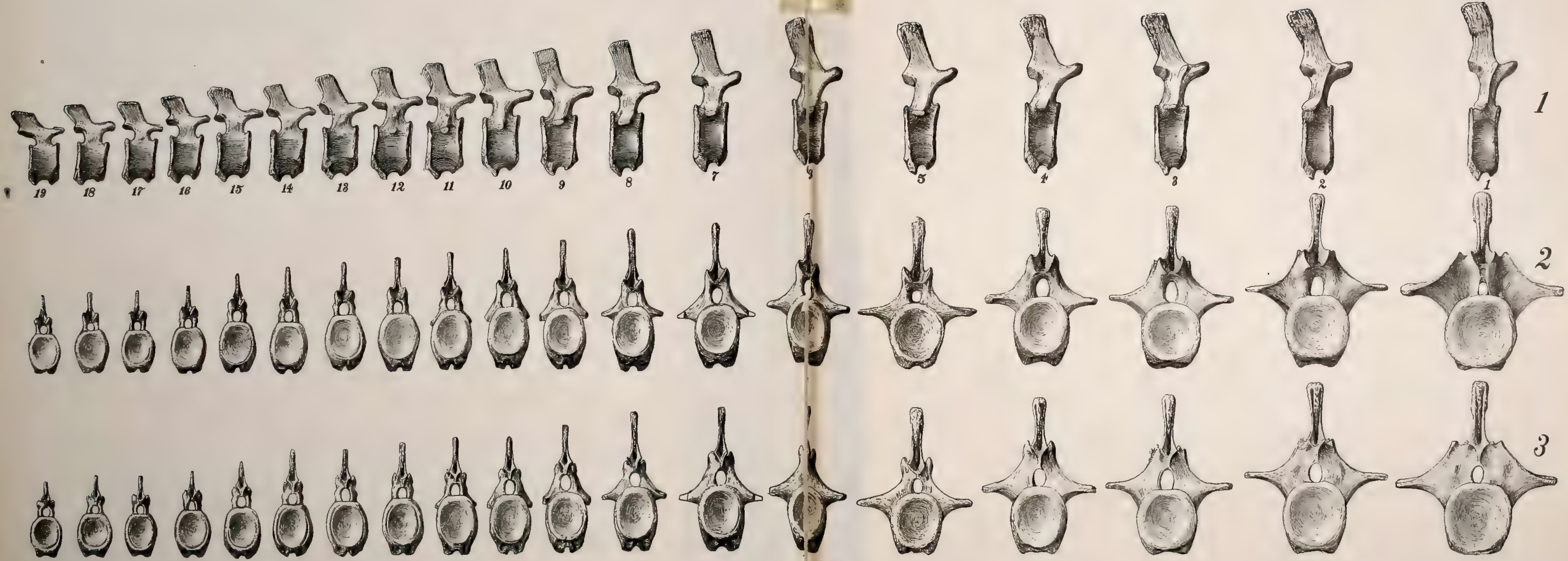
SYDNEY PRENTICE DEL.

NINETEEN ANTERIOR CAUDALS OF TYPE OF *HAPLACANTHOSAURUS PRISCUS*. 1,

PLATE III.

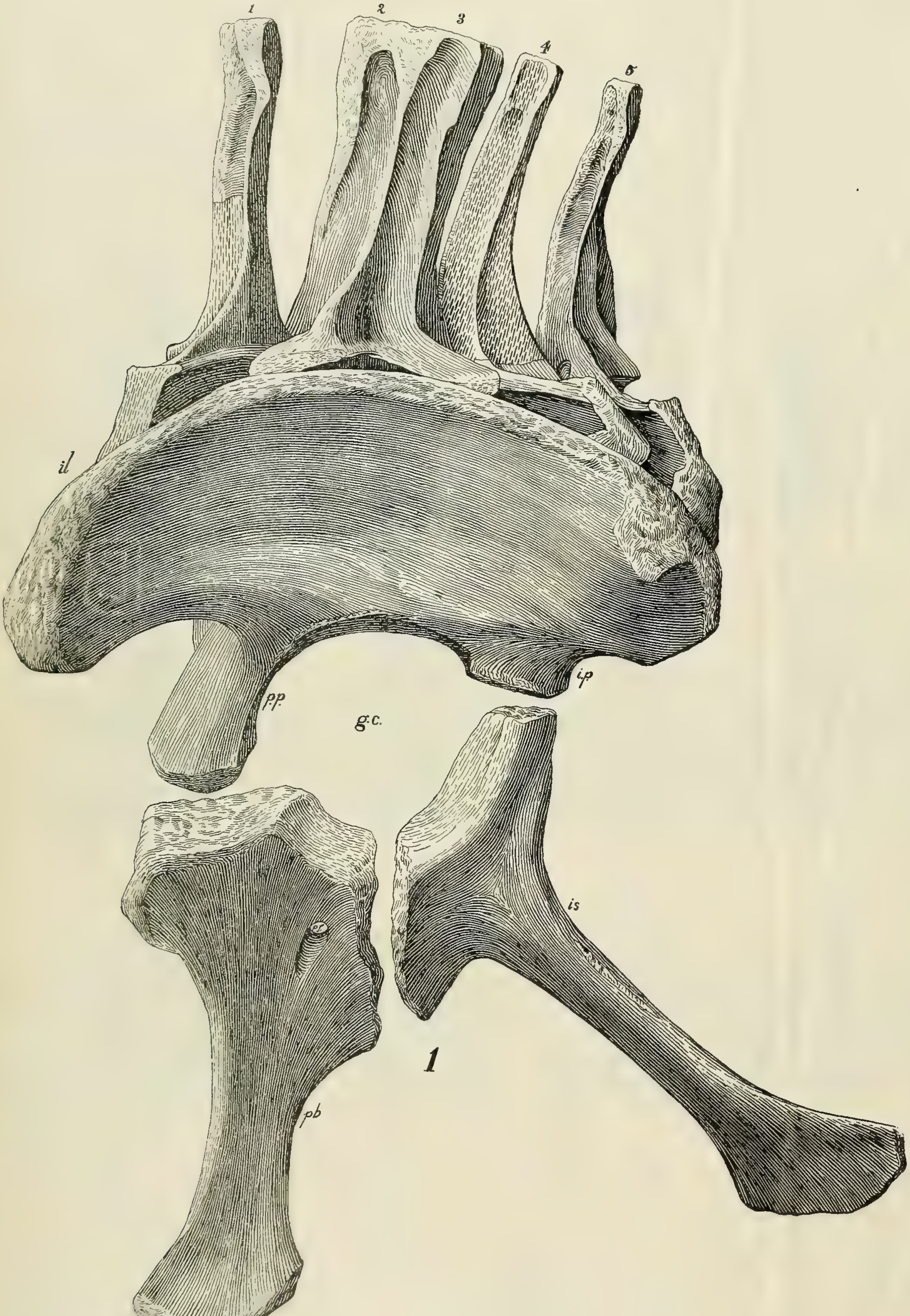


iew ; 2, Anterior view ; 3, Posterior view. $\frac{1}{10}$ Nat. size. (No. 572.)



SYDNEY PRENTICE DEL.

NINETEEN ANTERIOR CAUDALS OF TYPE OF *HAPLACANTHOSAURUS PRISCUS*. 1, SIDE VIEW; 2, ANTERIOR VIEW; 3, POSTERIOR VIEW. $\frac{1}{10}$ NAT. SIZE. (No. 572.)

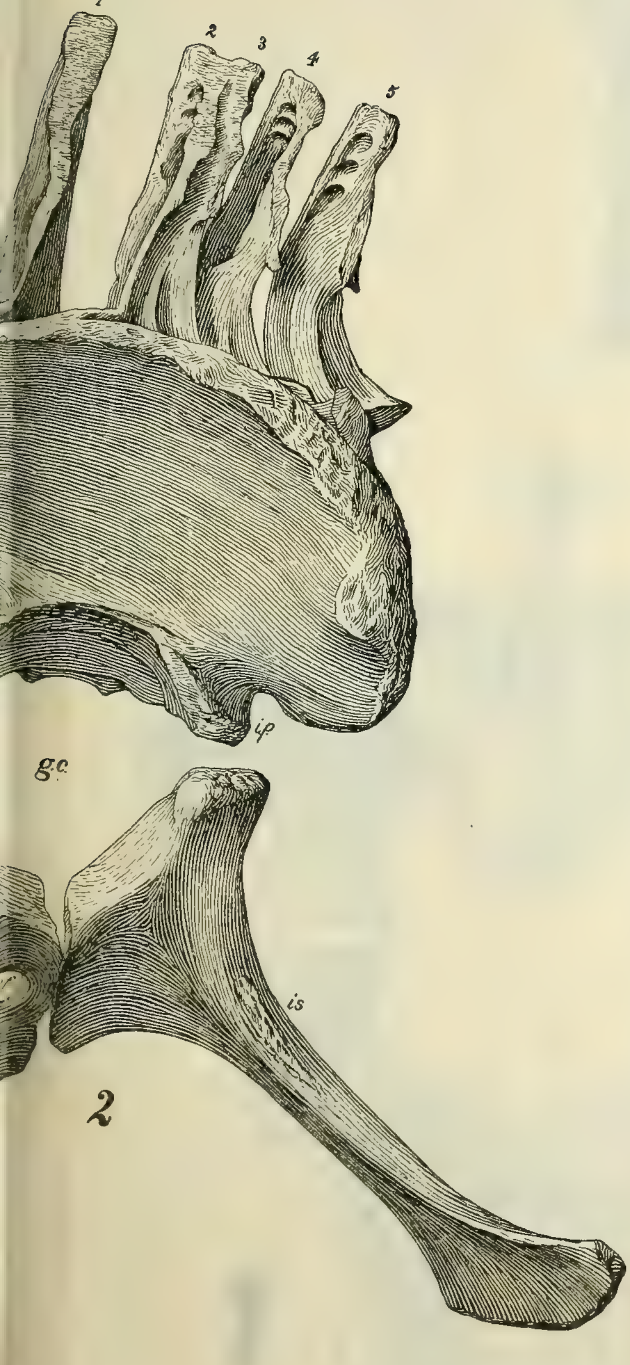


1

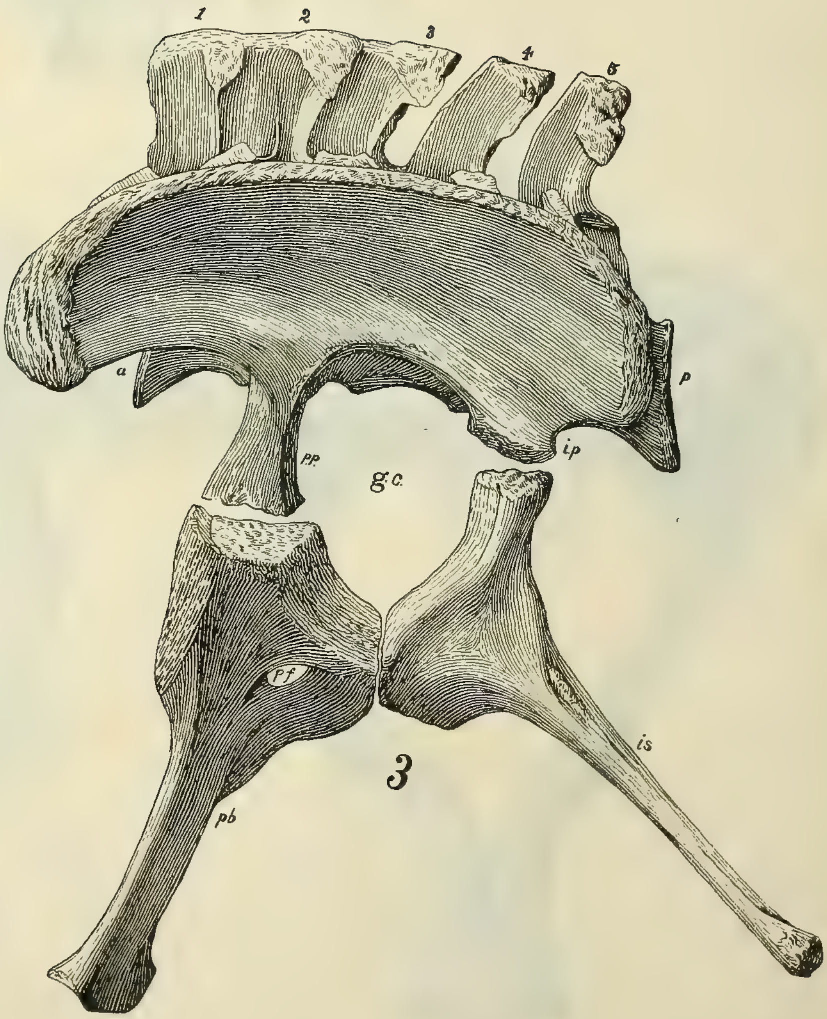
SYDNEY PRENTICE DEL.

1, PELVIS OF *BRONTOSAURUS*; 2, PELVIS OF *DIPLODOCUS*; 3, PELVIS O

PLATE IV.

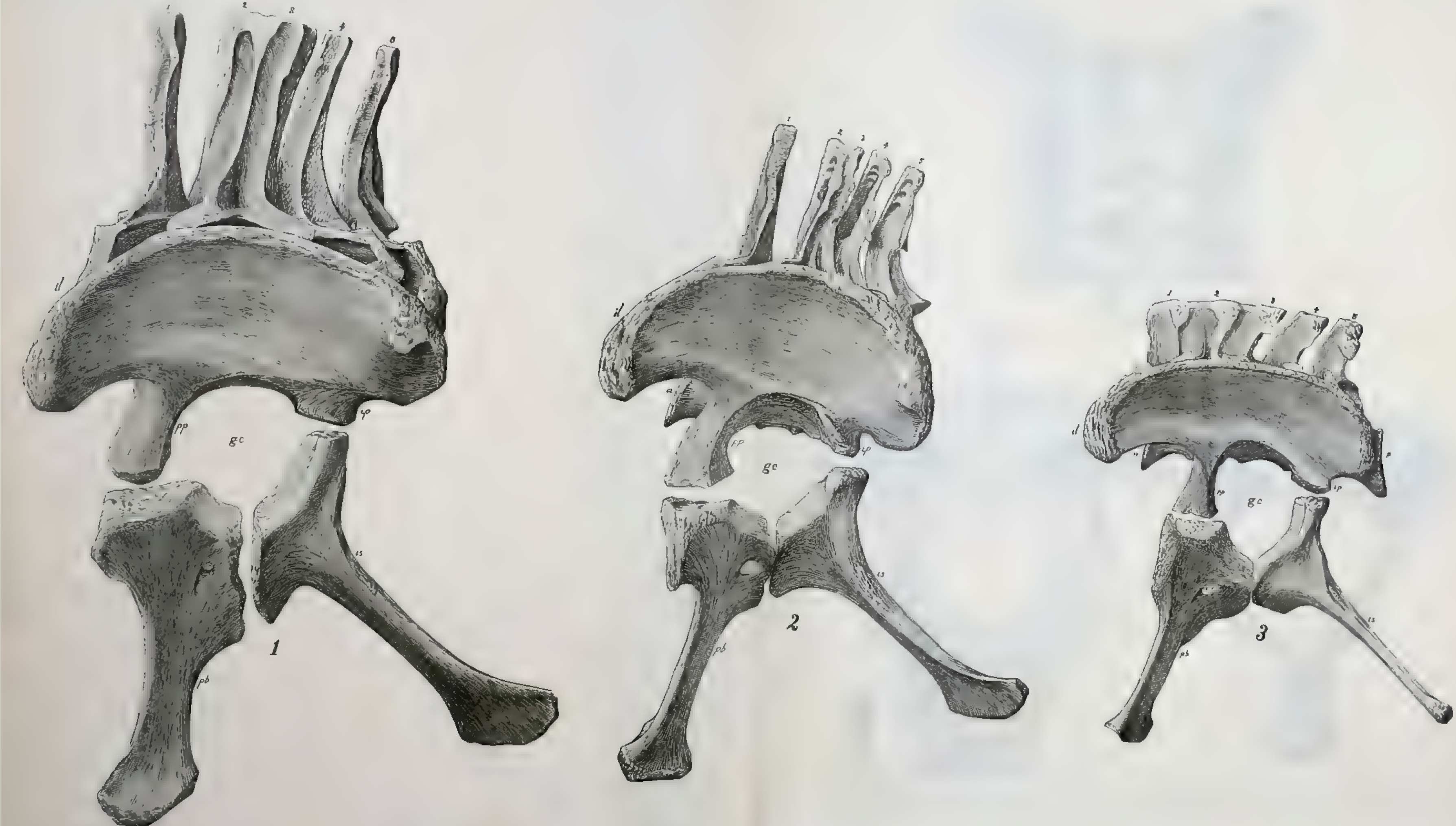


2



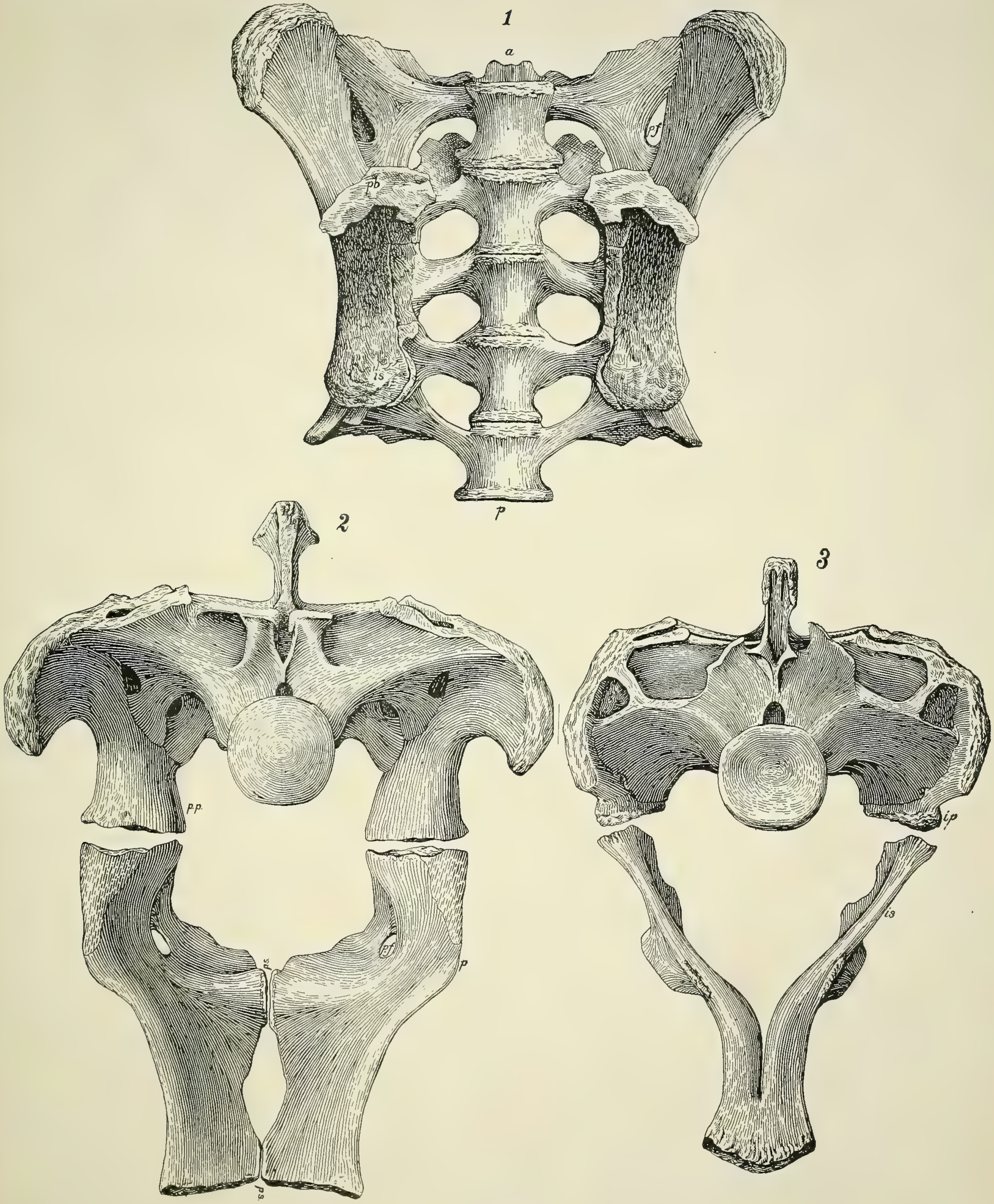
3

APLACANTHOSAURUS. All seen from left side. $\frac{1}{10}$ Nat. size.



SYDNEY PRENTICE DEL.

1, PELVIS OF *BRONTOSAURUS*; 2, PELVIS OF *DIPLODOCUS*; 3, PELVIS OF *H PLACANTHOSAURUS*. ALL SEEN FROM LEFT SIDE. $\frac{1}{10}$ NAT. SIZE.

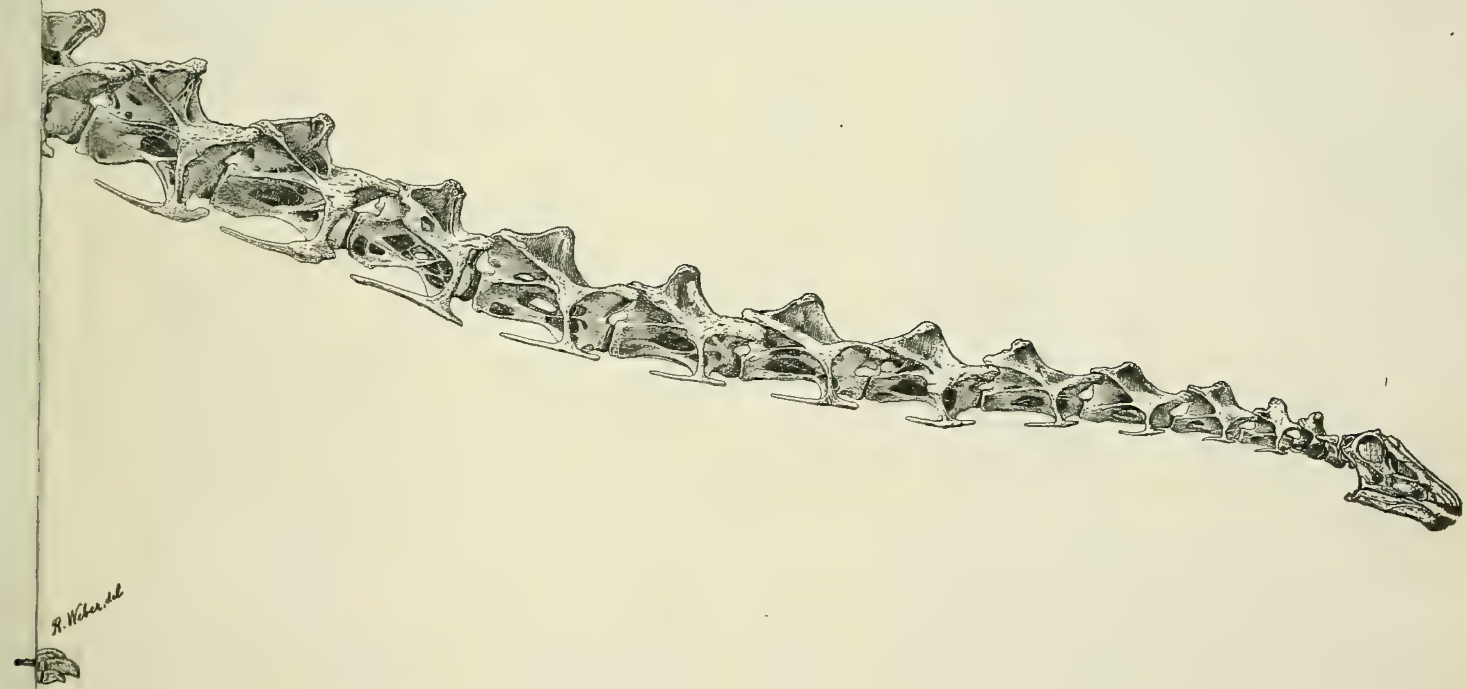


SYDNEY PRENTICE DEL.

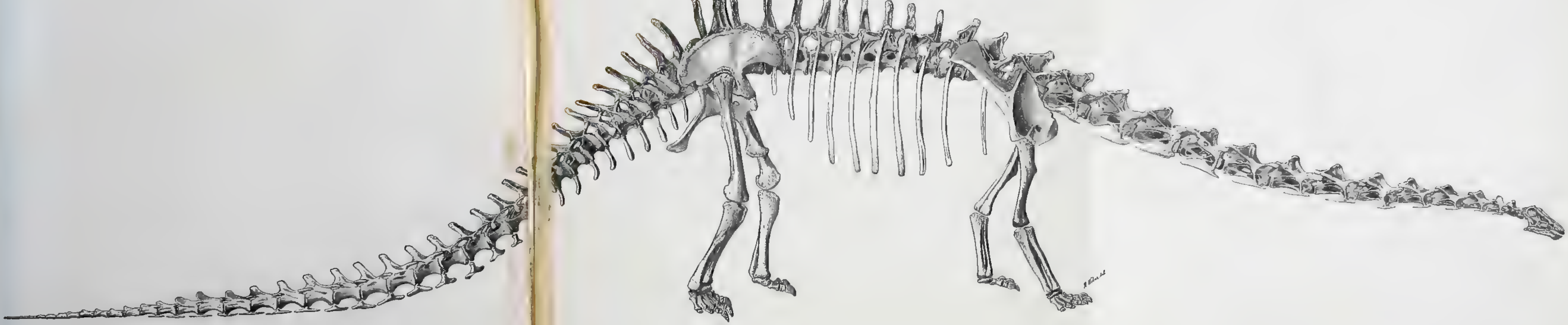
PELVIS OF TYPE OF *HAPLACANTHOSAURUS PRISCUS*. 1, INFERIOR VIEW; 2, ANTERIOR VIEW; 3, POSTERIOR VIEW. ALL $\frac{1}{10}$ NAT. SIZE. (No. 572.)

ME

PLATE VI



R. Weber del.



Restoration of *Diplodocus carnegii.* $\frac{1}{30}$ Nat. size.

Publications of the Carnegie Museum. Serial Nos. 30, 31, 32, and 35.

MEMOIRS
OF THE
CARNEGIE MUSEUM.

VOL. II. NOS. 2, 3, 4 AND 5.

W. J. HOLLAND, EDITOR.

---

2. OSTEOLOGY OF BAPTANODON MARSH.

BY C. W. GILMORE.

3. FOSSIL AVIAN REMAINS FROM ARMISSAN.

BY C. R. EASTMAN.

4. DESCRIPTION OF NEW RODENTS AND DISCUSSION OF THE ORIGIN OF DÆMONELIX.

BY O. A. PETERSON.

5. THE TERTIARY OF MONTANA, PARTS I, II.

BY EARL DOUGLASS

PITTSBURGH.
PUBLISHED BY THE AUTHORITY OF THE BOARD OF TRUSTEES OF THE
CARNEGIE INSTITUTE.
MARCH, 1905.

PRESS OF
THE NEW ERA PRINTING COMPANY,
LANCASTER, PA.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 2.

OSTEOLOGY OF BAPTANODON (MARSH).

BY C. W. GILMORE.

INTRODUCTION.

The discovery of the existence in the Jurassic of North America of a representative of the Ichthyosaurian reptiles was first announced by Professor O. C. Marsh in 1879.[1] Although fossil remains of these animals are very abundant in Europe where they have attracted the attention of naturalists for the past two centuries, with one exception[2] it was not until this late date that they were reported from this country. Notwithstanding that continued explorations in the Jurassic have brought to light many representatives of this group, with the exception of a few short papers nothing has been published concerning the skeletal features of these interesting reptiles.

The skeletons are usually imbedded in exceedingly hard and refractory concretions and the bone is so thoroughly impregnated with the matrix, which it closely resembles in color and texture, that the work of preparation is exceedingly tedious. The difficulty in preparing the material for study may in a measure account for the apparent neglect of this group.

The Jurassic Ichthyosaurian material preserved in the vertebrate collections of this museum has been largely gathered by the different field parties which have been operating for the past five seasons in the fossil deposits of the west.

Through the courtesy of Mr. J. B. Hatcher, late Curator of the Department of Vertebrate Paleontology of the Carnegie Museum, this material has been placed at the disposal of the writer for study and description.

---

[1] Marsh, O. C., "A New Order of Extinct Reptiles (*Sauranodonta*) from the Jurassic of North America," *Amer. Jour. Sci.* (3), Vol. XVII., pp. 85–86, January, 1879.

[2] Leidy, Joseph, "Notice of Some Reptilian Remains from Nevada," *Proc. Acad. Nat. Sci. Phila.*, Vol. XX., pp. 177, 178, 1868. A Triassic form.

The present paper is based upon the remains of three individuals, Nos.[3] 603, 878 and 919, from as many widely separated localities. All have been entirely freed from the matrix or worked out in relief by the writer and because of their remarkably well preserved condition several important osteological characters are shown for the first time.

In studying this material it was found necessary to compare it with the types of *Baptanodon*, preserved in the Yale Museum collections. Through the kindness of the late Dr. C. E. Beecher the author was permitted to study not only the types (*B. natans* and *B. discus*), but all of the Ichthyosaurian remains contained in the collections of that museum, comprising parts of some nine or ten individuals. At the American Museum of Natural History through the courtesy of Dr. W. D. Matthew I was given the privilege of examining the quite complete Jurassic Ichthyosaurian skeleton in that collection. Through my former instructor, the late Dr. W. C. Knight, I was accorded the privilege of studying the material at the Wyoming University, Laramie, Wyoming, part of which I helped collect. Thus practically all of the important Ichthyosaurian remains known from the Jurassic of North America have been personally examined during the preparation of this paper.

My acknowledgments are especially due the late Mr. J. B. Hatcher for the encouragement and kind consideration shown me in all matters pertaining to the preparation of this study.

For the preparation of the drawings used the author is grateful to the skill and patience of Mr. Sidney Prentice.

The photographs are by Mr. A. S. Coggeshall.

Occurrence and Distribution.

The Ichthyosaurian remains collected from the Jurassic of America have all been found in the upper part of the marine division of that formation. This marine strata was designated by Marsh as the *Baptanodon Beds*,[4] and included all of the Jurassic lying between the freshwater or *Atlantosaurus Beds* above and the red beds or *Triassic* (?) below. The *Hallopus Beds* of Marsh, if at all recognizable, have never been found in contact with the marine beds and their exact position in relation to these beds is yet undetermined.

Knight[5] has proposed the name Shirley for the marine series without assigning any place or giving any reasons for supplanting the old and generally accepted term *Baptanodon Beds*, which has priority.

---

[3] The numbers refer to the Card Catalogue of Fossil Vertebrates in the Collection of the Carnegie Museum.

[4] Marsh, O. C., "The *Reptilia* of the Baptanodon Beds," *Amer. Jour. of Sci.* (3), Vol. 50, pp. 405–406, 1895.

[5] Knight, W. C., Jurassic Rocks of Southeastern Wyoming," *Bull. of the Geol. Soc. of America*, Vol. XI., pp. 377–388, May, 1900.

Dr. F. B. Loomis[6] in a later paper proposes to confine the term *Baptanodon Beds* to the single layer in which the remains of these reptiles are found. Hatcher[7] has justly contended that the duplication by giving new names to old and well known formations, "tends to augment still further the confusion which already exists in our geologic formation names," and this would appear to be another instance in which the old and generally accepted term should be retained in its original meaning.

These beds have been briefly described by Knight as follows:[8] "Composed of bands of shale, limestone, sandstone, and clay. The limestones are usually shaly. The limestone beds are quite thin, but usually fossiliferous. The clays and shales usually contain large concretions which contain both vertebrate and invertebrate fossils. Septaria are common. The invertebrate as well as the vertebrate faunas are only partly known. This has been largely due to the fact that the richest fossil localities are where the concretions are well developed and until recently not many of these were known."

The following is a fairly complete list of the fossils described from the marine Jurassic of this country.

INVERTEBRATES.

Astarta packardi, White.
Belemnites densus, M. & H.
Cardioceras cardiformis, M. & H.
Cardioceras cardiformis, var. *distans*, Whitf.
Comptonectes bellistriata, Meek.
Comptonectes extenuata, M. & H.
Gryphæa nebrascensis, M. & H.
Dentalium subquadratus, Meek.
Goniomya montanaensis, Meek.
Grammatodon inornatus, M. & H.
Lima sp.
Lingula brevirostris, M. & H.
Modiola sp.
Ostrea engelmanni, Meek.
Pentacrinus asteriscus, M. & H.
Pholodomya kingi, Meek.
Pleuromya subcompressa, Meek.
Pinna sp.
Pseudomonotis curta, Hall.
Pseudomonotis orbiculata, Whitfield.
Tancredia cf. *extensa*, White.
Tancredia cf. *inornata* (M. & H.), Whitf.
Tancredia warrenana, M. & H.
Thracia weedi, Stanton.

VERTEBRATES.

Baptanodon natans, Marsh.
Baptanodon marshi, Knight.
Baptanodon discus, Marsh.
Cimoliosaurus laramiensis, Knight.
Megalneusaurus rex, Knight.
Plesiosaurus shirleyensis, Knight.
Pantosaurus striatus, Marsh.

---

[6] Loomis, F. B., "On Jurassic Stratigraphy in Southeastern Wyoming," *Bull. of Am. Museum of Nat. History*, Vol. XIV., article XII., pp. 189–197, June, 1901.

[7] Hatcher, J. B., *Memoirs of Carnegie Museum*, Vol. II., No. 1, November, 1903, p. 67.

[8] *Lit. cit.*, p. 385.

Two fishes have been referred to by Knight as probably coming from these beds.

Amiopsis dartoni, Eastman. *Pholidophorus americanus,* Eastman.

Hatcher[9] gives the geographical extent of these beds as follows: "The marine *Baptanodon Beds* throughout Wyoming and South Dakota are everywhere found accompanying and underlying the freshwater *Atlantosaurus Beds* though thinning out toward the south and entirely disappearing as we approach the Wyoming and Colorado state line." He has also shown that the lowermost 150 feet of the Jura at Cañon City, Colorado, may be the freshwater equivalents of the marine *Baptanodon Beds* farther north.

By far the largest number of skeletons of *Baptanodon* now known have been collected from the exposures of southeastern Wyoming, though several individuals have been discovered in the strata farther north. There is one specimen (No. 919) in the collections of this museum from the marine beds of north central Wyoming. Their remains are also reported from South Dakota.

Of the dozen or more specimens I have collected or helped collect every one was found more or less enclosed in one of those concretionary masses spoken of by Knight, the form and size of these concretions being dependent upon the shape and position of the skeleton enclosed. When exposed to the atmosphere, as often happens by the carrying away of the surrounding shale or clay, the concretion invariably cracks into an innumerable number of pieces.

It has been my experience that the anterior portion of the snout, the end of the tail and tips of the extremities are not enclosed by the concretion, and when present are found in the soil surrounding the rock. This will account for the poorly preserved condition of these parts in the material under discussion. Of the six skulls and parts of skulls examined the tip of the beak is wanting in every instance, and peculiar as it may seem, the anterior fourth of each protruded from the concretion into the surrounding shale. The quite complete posterior caudal series preserved in the collection of the University of Wyoming came from the clay. Four paddles have been studied and although the bones of the proximal segments are retained in their relative positions in the matrix, the distal part is wanting in every instance. In one example, the type of *B. discus* (No. 1955),[10] quite a number of the smaller or distal disks were preserved but their color and state of preservation indicated that they had come from the soft clay surrounding the concretion which contained the skeleton proper.

---

[9] *Lit. cit.*, p. 70.

[10] Catalogue number of the Yale Museum.

So far as I am able to learn there has never been more than a single individual found in any one of these concretions.

Plate VII. shows the outline of the concretion with the bones of specimen No. 878 in their relative positions as they lay imbedded in the matrix. The skull was lying on the right side and turned at a right angle to the vertebral column.

The snout projected from the concretion as explained above. The cervicals immediately following the atlas and axis were crushed into the left orbit so completely that it was deemed inadvisable to attempt their removal. In the course of preparation the skull has been separated from the block containing the other parts of the skeleton. Though slightly displaced the anterior 15 vertebræ are well preserved. The remaining six of the series are only represented by fragments and these are of little value for purposes of study.

The coracoids and scapulæ, as will be seen, were in their natural positions and give an accurate idea of the manner in which they articulated. The clavicles and interclavicle were somewhat removed from the remainder of the girdle, though the relation of these bones is very well shown. There are many parts of ribs but none are complete. The proximal end of the right humerus is the only limb bone represented and this end was only slightly removed from the glenoid socket.

The bones shown in this diagram will be referred to later in the detailed description of the several parts.

This specimen (No. 878) was collected by Dr. J. L. Wortman and party during the summer of 1899 on Troublesome Creek, Carbon Co., Wyo. It is the most complete individual of the three considered in this paper, and is unique as being the first to have the clavicles and interclavicle preserved. The parts of this skeleton preserved consist of a good skull and lower jaws, with a series of 21 vertebræ immediately posterior to the skull, the complete pectoral girdle, with the proximal extremity of the right humerus, numerous parts of ribs and isolated paddle bones.

The second individual (No. 603)[11] is from the *Baptanodon Beds* of Sheep Creek, Albany Co., Wyo. It was collected by Mr. O. A. Peterson and party during the season of 1900. The parts recovered consist of a nearly complete skull and lower jaws, numerous vertebræ and pieces of ribs, with a few paddle bones.

(No. 919) is from the Red Fork of Powder River, Big Horn Co., Wyo., and was collected by Mr. W. H. Utterback in 1902. The incomplete pectoral girdle and numerous vertebræ are represented. The dorsal and anterior views of the girdle are shown in Pl. XII.

---

[11] Hatcher, J. B., "The Carnegie Museum Paleontological Expeditions of 1900," *Science*, N. S., Vol. XII., No. 306, pp. 718–720, Nov., 1900.

Considering our limited knowledge of the structure of the Jurassic Ichthyosaurians, I shall figure and describe this material in detail.

The following description of the several elements is based largely on No. 878 supplemented by such characters as are shown by Nos. 603 and 919. Unless otherwise stated the material should be considered as pertaining to No. 878.

THE SKULL. (Pl. VIII.; Pl. IX., Figs. 1 and 2; Pl. X., Figs. 1 and 2; Pl. XI., Figs. 1 and 2.)

In general form the skull of *B. discus* bears a close resemblance to the other members of the Ichthyosauria. This is strikingly illustrated by the position and enormous size of the orbit, the presence of ossified sclerotic plates, the elongated nasals and premaxillaries and the reduced maxillaries.

Seen from the side the skull[12] is triangular in outline. The anterior portion is formed by the elongated rostrum observed also in many of the European species. The orbital opening is a conspicuous feature of this aspect of the skull; it is very large and nearly circular in form; its greatest vertical diameter is 241 mm. the horizontal diameter being 234 mm. It is enclosed above by the post- and pre(?)-frontals, posteriorly by the postorbital, below by the jugal, and anteriorly, chiefly by the lachrymal. Just anterior to the orbit is the obliquely placed narial opening. In skull No. 603 these openings appear to be more nearly horizontal (see Pl. X., Fig. 2) as is generally observed in *Ichthyosaurus*. The nares are bounded by the nasals, prefrontals (?), lachrymals, maxillaries, and premaxillaries.

Viewed posteriorly (see Pl. XI.) the skull is subrectangular in form being wider than high. This aspect shows this region to be more compactly and firmly constructed than in any known form of the Ichthyopterygia. The arrangement of the opisthotics and stapes is such as to give the greatest strength and rigidity to this region. They act as braces from the basioccipital as a fixed point to all four angles of the skull. In comparing this view of the skull of *Baptanodon* with those of *Ichthyosaurus* as shown by Cuvier,[13] Owen,[14] Cope,[15] Frass,[16] Bauer[17] and Woodward,[18] the great solidity of the former contrasts strongly with the loose and weak arrangement seen in the latter.

---

[12] All drawings of the skull with the exception of the inferior view, Plate IX., Fig. 2 (No. 603), have been made from specimen No. 878, though for the sake of completeness, elements and sutures not discernible in this specimen, when present, have been supplied from No. 603. Whenever such use has been made mention is given in the detailed description of the elements to appear later. Dotted lines indicate the probable position of sutures not shown by the material at hand.

[13] Cuvier, R., "Ossemens Fossiles," Vol. 6, Plate XXIX.

[14] Owen, R., "Monograph of Fossil Reptilia of the Liassic Formations," Pt. III., Plate XXVI.

[15] Cope, E. D., "On the Homologies of some of the Cranial Bones of the Reptilia," *Proc. Am. Assoc.*, Vol. XIX. fig. 2, p. 199.

[16] Frass, E., "Die Ichthyosaurier der Süddeutschen Trias und Jura Ablagerungen," Plate II., figs. 3–8.

[17] Bauer, Franz, *Anatomischer Anzeiger*, Vol. XVIII., p. 586, fig. 17, 1900.

[18] Woodward, A. S., "Vertebrate Palæontology," fig. D, p. 178.

The foramen magnum is the largest opening in this view of the skull. It is subelliptical in form with the greatest diameter vertical. The opening is bounded by the basi-occipital below, exoccipitals and supraoccipital laterally, and supraoccipital above. There may have been a foramen, see Pl. XI., figs. 1 and 2, between the exoccipital, opisthotic, parietal and squamosal, though this cannot be absolutely determined from the material at hand. The small elongate opening formed by the quadrate and quadratojugal is the "auditory meatus" of Owen.

The superior view of the skull has the triangular form seen in the lateral aspect. Posteriorly on either side of the brain case are the large temporal vacuities surrounded by the squamosals, parietals, post- and pre-(?) frontals. It will be noticed that the sutures between the parietals, frontals and posterior part of the nasals, as indicated by the dotted lines are obliterated in these specimens. A pineal foramen appears to be present in both of the skulls before me.

The inferior region posteriorly is well preserved in both skulls but more anteriorly the determination of the different elements has been rendered difficult by the crushing to which the specimen was subjected.

The palate view as shown in Pl. IX., fig. 2, has been drawn almost entirely from the skull pertaining to specimen (No. 603).

Medially there is the long interpterygoid vacuity enclosed laterally by the inner borders of the pterygoids and posteriorly by the basisphenoid. This vacuity is divided posteriorly by the long slender process of the presphenoid.

Because of the close attachment of the lower jaw the size and extent of the pterygomalar vacuity cannot be determined from these skulls. Owing to lateral compression the posterior nares have been nearly closed and their exact shape cannot be determined.

MEASUREMENTS OF THE SKULLS.

No. 878.	Greatest	length	of skull	1082	mm.
" 603.	"	"	"	1028	"
" 878.	"	width	"	315	"
" 603.	"	"	"	222	"
" 878.	"	height	"	320	"
" 603.	"	"	"	295	"

Basioccipital (*b.occ.*). — The basioccipital is a short heavy bone the most robust element of the posterior portion of the skull. It extends backward forming a subcircular convex condyle, which superiorly is separated from the foramen magnum by a very narrow nonarticular tract. This tract as it descends is concave and gains breadth in flaring out to meet the investing bones. As usual it is separated from the articular tract of the condyle below by a very shallow groove. In both specimens (Nos. 603 and 878) inferiorly there is a very prominent transverse dividing line, which probably represents the deep vertical suture between the basioccipital and basisphenoid. In either instance however the size of the suture has probably been exaggerated somewhat by crushing. On the median neural surface there is a shallow antero-posterior channel which forms the basal boundary of the foramen magnum, and on either side are deep excavations for the sutural articulations with the exoccipitals. These elements do not enter into the composition of the occipital condyle as in some reptiles.

Principal measurements are as follows:

No. 878.	Greatest breadth of occipital condyle	65 mm.
" 603.	" " " "	65 "
" 878.	" depth " "	58 "
" 603.	" " " "	64 "
" 878.	" breadth of basioccipital	90 '
" 603.	" " "	90 "
" 878.	" depth "	74 "
" 603.	" " "	85 "
" 878.	" length "	60 "
" 603.	" " "	62 "

Exoccipitals (*ex.occ.*). — These elements viewed from the back are seen as two small subrectangular bones that rise from the superior surface of the basioccipital to support the heavy inverted U-shaped supraoccipital. The interior margins of these bones form the walls of the lower third of the foramen magnum. Below the articular ends are somewhat enlarged for the strong sutural articulation with the basioccipital. The external surfaces are very slightly concave transversely. These elements do not show the lateral excavations seen in the exoccipitals of *Ichthyosaurus*, but apparently there is a foramen at this point as in the former genus though this cannot be definitely determined from our specimens.

MEASUREMENTS.

No. 878.	Greatest length of exoccipital	34 mm.
" 878.	" breadth "	25 "

Supraoccipital (*s.occ.*). — Of the four bones forming the boundary of the foramen magnum the supraoccipital contributes the greater part. This element as seen posteriorly has the form of an inverted U, the stems of which articulate with the exoccipitals. The supraoccipital of *B. discus* differs materially from the corresponding element in *Ichthyosaurus*. In the latter genus the supraoccipital is a remarkably massive bone which only enters slightly into the formation of the foramen magnum, hardly more than arching over the superior boundary.

The supraoccipital and exoccipitals do not maintain a vertical position as in most reptiles, but are inclined forward at a considerable angle. The superior and lateral surfaces of the former being wedged in between and under the overlying parietals, not grown fast with them but as in *Ichthyosaurus* only held there by ligaments or cartilage. The posterior face from the edge of the foramen to where it passes under the parietals presents a slightly rounded surface. On the superior median surface this element is slightly enlarged, see Pl. XI., fig. 1 and 2, resembling somewhat the complete symphysis of a suture, which suggests the idea that these elements might have been paired at one time. The articular ends are triangular in form with the central portion slightly concave.

It may be of interest to note that the part this element takes in the formation of the foramen magnum, *i. e.*, the triangular form of the articular face for the exoccipital and the suggestion of having been paired at one time, it resembles the Plesiosaur (*Dolichorhynchops osborni*)[19] more than any other form of reptile that has come under the observation of the writer.

MEASUREMENTS.

No. 603.	Greatest height of supraoccipital	70 mm.
" 878.	" " "	65 "
" 878.	" width "	26 "

Opisthotic[20] (*op.o.*).—The opisthotics are two subcylindrical bones that extend outward and upward from the lateral superior surfaces of the basioccipital, broadest where they meet the basioccipital, exoccipital and stapes, constricted medially, again expanding into a rounded end which abuts against and between that portion of the squamosal where it divides into a superior and inferior branch. The squamosal really encloses the upper half of these elements. The lower articular end has three distinct articular faces which unite with the exoccipital, basioccipital and stape respectively. It will be observed in Pl. XI., fig. 1, that the right opisthotic is somewhat removed from what I have considered as the normal position shown by the left element. The relations and shape of these elements differ considerably from the opisthotics in *Ichthyosaurus*. Here we find the upper or superior end articulating with the squamosal and not free as shown by most of the illustrations of this view of the skull of *Ichthyosaurus*.

[19] Williston, S. W., "North American Plesiosaurs," Part I., Field Columbian Museum, Publication 73, Geol. Series, Vol. II., No. 1, fig. 3, p. 27.

[20] It has been shown by Dr. S. W. Williston that this element if a single bone should be called the paraoccipital which is the older name given to this bone by Owen in 1838. But until better understood I use the generally accepted term opisthotic, *lit. cit.*, p. 25.

In *Ichthyosaurus* the lower articular end is shown as only articulating with two bones, the basioccipital and exoccipital, the stronger surface being opposed to the latter. In *B. discus*, as has been indicated above, this bone articulates with three elements the longest face being opposed to the basioccipital.

Woodward[21] shows the opisthotic of *I. longifrons* as articulating exclusively with the exoccipital and instead of extending outward and upward, it is inclined outward and slightly downward reaching the inner border of the quadrate. In his diagram the stapes are absent. Frass[22] gives a posterior view of the skull of *I. quadrissicus* in which the opisthotic articulates medially with the exoccipital and slightly if at all with the basioccipital. Outwardly the upper end is free. In this species the parietal is interposed between the free end of the opisthotic and the squamosal. Cope's[23] diagram of this view of the skull of *Ichthyosaurus* approaches the form under consideration more nearly than any brought under the writer's observation. Though Cope was probably mistaken in the placing of the stapes as not articulating with the basioccipital.

MEASUREMENTS.

No. 878.	Greatest length of opisthotic	60 mm.
" 878.	" breadth distally of opisthotic	40 "
" 878.	" " proximally of opisthotic	27 "

Stapes (*st.*).—The stapes are two trihedral bars that extend downward and outward from the lateral inferior borders of the basioccipital. The superior or articulating end is the most expanded, being divided into two distinct articular faces. The upper face is opposed to a similar articular surface on the opisthotic at about the middle of the side of the basioccipital. The lower articular surface is in contact with the lower side of the basioccipital. The outer end of this bone is slightly expanded and rests in a groove on the inner lower posterior surface of the quadrate. The position assigned it by Baur[24] in the Ichthyosauria. Seen posteriorly the surface is slightly rounded. Viewed from the outer end this bone is triangular in form. Above, the inferior bar of the squamosal comes down and passes under the superior lateral margin. The lower side apparently, rested upon the posterior superior surface of the pterygoid. The foramen shown in all posterior views of the skulls of Ichthyosauria which I have studied appears to be entirely closed by the inferior branch of the squamosal in *B. discus*. Although by an examination of the different views referred to above, hardly any two agree in the exact shape and position of these openings, furthermore, it would appear that nearly if not all of these figures are either diagrammatic or drawn from reconstructed material which may explain some of the otherwise unaccountable differences, not only between the forms of the two genera compared here, but in species of the genus *Ichthyosaurus*. Differences which if present should certainly be considered as of more than specific importance.

---

[21] Woodward, *lit. cit.*, p. 178, fig. 111.

[22] Frass, *lit. cit.*, Plate II., figs. 3–8.

[23] Cope, *lit. cit.*, p. 199, fig. 2.

[24] Baur, G., "On the Morphology and Origin of the Ichthyopterygia," *Amer. Nat.*, Vol. XXI., 1887, p. 837.

Cope[25] in 1870 was the first to recognize and correctly determine the opisthotic and stapedial bones in *Ichthyosaurus*. Since then, however, as shown above some authorities have given posterior views with the stapes absent.

MEASUREMENTS.

No. 878.	Greatest length of stapes	70 mm.
" 878.	" breadth of proximal end	47 "
" 878.	" " distal end	25 "

Squamosal (*sq.*). — In the nomenclature of this bone the usual determination is followed. Both Baur and Merriam reverse the names of the two bones here designated as *squamosal* and *supratemporal*. The element here called squamosal is the *mastoid* of Owen.

The squamosal is a large irregular triradiate bone, the upper part of which forms the superior posterior angle of the cranium. From a posterior obtuse central portion three branches are given off. The internal branch, the most robust part of the element extends forward and upward from the angle of the skull to meet the lateral posterior margin of the descending parietal. Superiorly the surface is thickened and rounded and forms the posterior boundary of the supratemporal fossa. Seen posteriorly it is a flattened subtriangular plate the base of which laps over the upper lateral margin of the opisthotic. The inferior plate superiorly is deeply indented by the intrusion of the superior end of the opisthotic, or in reality this element is opposed to the squamosal at the junction of the internal and inferior parts. The inferior branch as it descends widens into a broad flat plate that completely fills all of the space between the opisthotic, stapes and quadrate, its lower extremity passing under the upper lateral margin of the stapes. The outer border unites with the inner border of the quadrate for the greater part of its length. Medially this plate is inclined forward, its inner margin underlapping both the opisthotic and stape. The superior outer margin is continued upward along the quadrate to meet the supratemporal at the angle of the skull. The anterior branch of the squamosal is greatly compressed from side to side. This thin plate is directed forward and inward, and forms about one half of the outer boundary of the temporal fossa. Although it is produced along the inner side of the postfrontal by an elongated suture, this part inferiorly meets the supratemporal and the posterior portion of the postfrontal. The squamosal as in Reptilia and Batrachia generally forms part of the combination which supports the quadrate. This bone articulates with the quadrate, parietal, opisthotic, supratemporal and postfrontal.

---

[25] Cope, E. D., *lit. cit.*, p. 247.

MEASUREMENTS.

No. 878.	Greatest length of anterior branch of squamosal	128 mm.
" 878.	" " internal " "	76 "
" 878.	" " inferior " "	90 "

Supratemporal (*s.t.*). — The supratemporal is an irregular subtriangular bony plate that is wedged into the interspace between the squamosal, post-frontal, postorbital, quadratojugal and quadrate. Externally the surface is slightly convex. This bone represents the *prosquamosal* or *supersquamosal* of Owen, the *temporal* of Cuvier, the *squamosal* of Baur and Merriam, and the *supraquadrate* of Seeley; the latter name being given because it rests upon and hides from lateral view the upper portion of the quadrate. The terms enumerated have been used in describing the more primitive forms contained in the genera *Shastasaurus* and *Ichthyosaurus*.

Quadrate (*qu.*). — The quadrate viewed posteriorly is a flat narrow vertical plate with the external margin excavated. In conjunction with the quadratojugal it enclosed the auditory opening as in *Sphenodon*. Superiorly this element meets the supratemporal and squamosal, the latter assuming the greater part of the articulation as will be found to be the case in most of the Ichthyosaurs. The quadrate expands distally into a heavy transverse articulation for the lower jaw.

In specimen No. 878 the lateral separation between the quadrate and inferior branch of the squamosal is distinctly shown on both sides of the skull, see Pl. XI., fig. 1, but on the left side of the skull of No. 603 the suture has become obliterated and the two bones thus united form a continuous broad plate of bone. Distally the external concave border turns abruptly outward. It is upon this border just internal to the articular end that the infero-posterior angle of the quadratojugal rests. The lower internal border of the quadrate unites closely with the postero-lateral process sent off by the pterygoid. On the lower posterior surface there is a slightly roughened groove which received the lower or distal end of the stapes. These elements have been somewhat displaced by crushing, and their normal relations cannot be definitely determined, though the presence of this groove has convinced the writer that the above was undoubtedly their natural position. See Pl. XI., fig. 2.

Specimen No. 603, which has the posterior portion of the right ramus wanting, gives a good view of the articular end of the quadrate. It is pentagonal in form, narrower antero-posteriorly than laterally and concave on the inner border where it meets the descending process of the pterygoid.

MEASUREMENTS.

No. 878.	Greatest length of the quadrate	122	mm.
" 878.	" width distal end of the quadrate	50	"
" 603.	" " " " " "	50	"
" 878.	" " antero-posteriorly of the quadrate	43	"
" 603.	" " " " " "	40	"

Quadratojugal (*q.j.*). — The quadratojugal seen from the side is a small triangular bone that connects the jugal and postorbital with the quadrate. The posterior border of this bone is slightly rounded; distally somewhat expanded, thus forming an articular end which meets the outer border of the quadrate at nearly right angles, resting upon this edge just above the heavy articular end of the latter.

The external surface is flat. The opposite side forms the outer boundary of the foramen at this point. Superiorly this element passes under the quadrate and supratemporal, the upper portion being hidden from a side view by the overlying postorbital. The infero-anterior border is united with the jugal by a suture 47 mm. long. The lower border of this bone is 57 mm. in length.

Postorbital (*pto.*).—The postorbital is a more slender element than the jugal, and as Owen[26] has observed "resembles a dismemberment of an ascending process of the malar." Its lower end overlaps and joins by squamous suture the posterior end of the jugal. This suture between the jugal and postorbital is 89 mm. in length, the same as given by Professor Seeley for the corresponding suture in *Ichthyosaurus* (*zelandicus*) *quadriscissus*.[27] As it rises to the middle of the back of the orbit the width remains about the same, above the middle it curves upward and forward along the lower margins of the supratemporal and postfrontal. Above the middle of the orbit the postorbital suddenly expands, then tapers to a slender point that terminates on the lower border of the postfrontal nearly at the top of the orbit. Viewed laterally the surface is slightly concave. The anterior border forms the posterior boundary of the orbit. This bone unites with the jugal, quadratojugal, supratemporal and postfrontal.

Sclerotic plates (*scl.*). — The sclerotic ring is unusally well preserved in at least one orbit of both skulls. In No. 878 the ring is composed of fourteen wedge-like plates, the inner ends being truncated by the pupillary opening.

From the pupillary border the plates extend outward ray-like to the periphery of the eyeball, there bending sharply inward completely enclosing the outer borders.

---

[26] Owen, R., *lit. cit.*

[27] Seeley, H. G. *Quart. Jour. Geol. Soc., of London*, Vol. XXXVI.

The matrix in this region has not been sufficiently removed to show fully the inward extension of these plates. The surface of each plate is covered with lines that radiate from the center of the plate inward and outward to either lateral border.

The ring is nearly circular in form and almost fills the large orbit. The pupillary opening measures about 100 mm. in diameter, the entire diameter of the ring being 202 mm. The left orbit of No. 603 has the ring nearly as well preserved, though the exact number of plates cannot be ascertained. The outer surface is inclined somewhat from the center to the outer margin and does not present so flat a surface as observed in a specimen (No. 877) of *I. communis* in the collection of this museum. The sclerotic rings do not stand parallel to one another but are inclined inward anteriorly.

Jugal (*j.*). — The jugal is a long curved bar that forms the lower boundary of the orbit. This element in both of the specimens under consideration is unusually strong. Anteriorly the end commences in a tapering point which is wedged in between the lachrymal and maxillary. Medially it widens into a subcompressed bar reaching its maximum width under the middle of the orbit. At this point superiorly the surface is slightly concave but becomes flattened and compressed posteriorly terminating in a wedge-like end which is received between the postorbital and quadratojugal.

Parietals (*pa.*). — In both skulls the median parietal sutures are entirely obliterated. The lateral surfaces which form the outer walls of the brain case are smooth, slightly concave antero-posteriorly and gently convex from the crest downward. The matrix has not been sufficiently removed from the temporal fossa to show the depth of the parietals or their relations to the lower bones of the brain case. The brain case is narrowest just posterior to the middle region but expands both posteriorly and anteriorly. The parietal foramen or pineal eye appears to be bounded posteriorly by the parietals and anteriorly by the frontals. Extending forward and outward from the lateral boundaries of the foramen are the sutures (?) that unite the parietals with the two small frontals. From the antero-internal angle of the temporal fossa the suture between the postfrontal (?) and parietal extends inward and forming an acute angle with the fronto-parietal suture.

The sagittal crest is indicated by a faint ridge posteriorly. The lower posterior border of the parietal rests upon the underlying supraoccipital without sutural junction. The posterior lateral extensions curve downward and backward descending to the top of the exoccipitals, thus contributing to the upper and lateral faces of the occipital surfaces. Seen posteriorly the median portion is slightly thickened, the lateral extremities narrowing somewhat as they descend to occupy the space between the internal branch of the squamosal and the supraoccipital.

Frontals (*fr.*).—The frontals are, so far one may rely on the very unsatisfactory evidence at hand, very small and in a general way resemble those elements observed in the skulls of the *Ichthyosauria* generally. The sutures of this region are quite indistinct being indicated by hardly more than fractures. These fractures however having been produced by pressure would naturally have followed the line of least resistance, which in this case is that of the sutural union of the different elements. As these fractures have the position and direction of the sutures shown in the drawings of Ichthyosaurian skulls I have had them drawn in provisionally. See Plates VIII. and IX. Because of the conjectural nature of the above evidence no attempt will be made to describe this region in detail. This portion of the skull of No. 603 is so badly crushed that all sutures have been entirely obliterated.

Postfrontal (*ptf.*).—The posterior border of this bone is well shown, but anteriorly as explained above the sutures are only indicated by transverse fractures. The post- and prefrontals will be considered here as a single element extending from the supratemporal behind to the rounded fracture forward where it unites with the elongated nasals. Although in *Ichthyosaurus* Frass shows a suture immediately over the eye separating the pre- from the postfrontal, there are no indications of such a suture in our specimens. Reynolds[28] says "The exact position of the suture between the prefrontal and postfrontal is not known." This element as here considered is a moderately long compressed bone forming the quite horizontal postorbital arch. Posteriorly the bone is obliquely inclined so that the outer surface looks outward and upward. Fore and aft the element is convex. The nearly square posterior end unites with the supratemporal, the postero-superior margin with the anterior branch of the squamosal, the latter being prolonged on the inner surface of the postfrontal which is united by an extended suture. The outer or inferior border at this end joins the upper border of the postorbital for about 63 mm., but more anteriorly this bone alone forms the upper boundary of the orbit, at this point assuming a nearly horizontal position. Anteriorly this element acquires its greatest width as it curves in front of the temporal fossa to meet the parietal and frontal. Though how much of this wide portion if any is prefrontal we cannot determine at this time. The superior surface in front of the temporal opening is elevated into a rounded transverse ridge which becomes narrower and somewhat depressed as it approaches the junction with the parietal. Anterior to this ridge the surface is slightly convex transversely and bends downward longitudinally to meet the nasals.

---

[28] Reynolds, "The Vertebrate Skeleton," p. 196.

Prefrontal (*prf.*).—The shape of the prefrontal, or even the probable outlines, cannot be determined from the present specimens. On the right side of the skull pertaining to specimen No. 878 is a narrow portion forming the upper and forward boundary of the orbit extending down to meet the lachrymal in front. The narrow portion just cited is undoubtedly a part of the prefrontal as this is the position of this element in all fully figured Ichthyosaurian skulls. Although Baur[29] says, "The lachrymal is free from the prefontal in *Ichthyosaurus,* as in many Lacertilians; it is united with this bone in *Sphenodon.*"

Nasals (*na.*).—The outline of these bones when viewed from above is triangular. They are elongate antero-posteriorly and form an acute angle where the two elements pass beneath the overlapping premaxillæ as shown by Owen[30] in *I. camplyodon.* The anterior sutural boundaries of these bones are best shown in the skull pertaining to specimen No. 603. Posteriorly and laterally the nasals are bent abruptly downward and form the outer surface of the skull in front of the orbit and above the nares. Anteriorly the outer surface is inclined less obliquely, gradually becoming convex as the nasals extend forward. Above, the nasals are widest at their posterior ends and in so far as one may judge from the damaged condition of this region they were somewhat concave transversely. Posteriorly the nasals united probably with the frontals and the prefrontals (?). The suture separating the nasal from the premaxillary begins at the upper anterior angle of the nasal opening and extends obliquely upward, forward and inward meeting its fellow medially at a point about one third the distance from the anterior to the posterior extremity of the skull. There is a small angular protuberance over the middle of the nares which I have not observed in other Ichthyosaurian skulls. The suture separating the nasals is plainly shown anteriorly in specimen No. 603. In the accompanying figure Pls. VIII. and IX., the anterior sutures have been drawn from that specimen.

Lachrymal (*la.*).—The lachrymal is a large subtriangular bone that joins the prefrontal (?) above and the jugal below to complete the anterior boundary of the orbit. The posterior border is concave. A spine-like prolongation extends backward beneath the eye and unites by suture with the anterior third of the jugal, this border more anteriorly meets the maxillary, terminating at the lower anterior border of the nasal opening. The superior process presumably, meets the prefrontal and nasals above. The latter probably as in *I.* (*zelandicus*) *quadriscissus* sending down a small projection posterior to the narine opening to meet it. Anteriorly the oblique superior border forms the lower boundary of the external nares. The facial surface posteriorly is somewhat concave and looks outward and backward; anteriorly it is somewhat rounded, sloping in toward the nasal opening. The inferior side is nearly straight though elevated obliquely from back to front.

---

[29] Baur, G., *lit. cit.*, p. 838.

[30] Owen, R., "British Cretaceous Reptiles," Monograph, 1851.

Maxillary (*mx.*). — The anterior half of the left maxillary of specimen (No. 603) was firmly fastened to a section of the left ramus by the intervening matrix and being separated from its position in the skull we have a splendid view of the form and structure of the anterior half of this bone. Laterally this element is subtriangular in outline. It commences posteriorly under the anterior border of the eye, from which it is separated by the anterior portion of the jugal and the posterior branch of the lachrymal. Anteriorly it expands into facial, alveolar and palatal aspects, again tapering out to a slender pointed anterior end. The complete outer anterior view is hidden by the enclosing premaxillary. The median superior margin contributes a part to the lower boundary of the nasal opening. On the median superior surface a long slender horizontal process is developed which fits into a corresponding depression in the premaxillary. The matrix has not been removed sufficiently from the inside to determine whether it articulated with other bones beside the palatines and premaxillaries in that region. Nothing is known of the upper part of the posterior extremity of the maxillary. Anteriorly the superior or articulating surface is rounded, being covered with longitudinal markings.

The inferior surface anteriorly is concave and forms the deepest portion of the alveolar groove.

Premaxillary (*pmx.*). — The premaxillæ are characterized as in nearly all Ichthyosaurians by their great length. In *B. discus* the posterior termination is forked as in many forms of this order. The lower posterior portion enclosed the anterior portions of the maxillary and hides it from a lateral view. From the anterior boundary of the nares the suture between the nasal and premaxillary extends forward and upward to where the opposite branches become confluent and cover the anterior extremities of the nasals. The anterior part of the snout narrows gradually to the end and is composed of the premaxillæ alone. The tip as has been already explained is wanting in all of our specimens. The sides are slightly flattened but above are convexly rounded. The median suture is obliterated in both specimens although the slipping of the two halves past one another in the skull belonging to No. 878, see Pl. X., fig. 1, indicates that such a suture existed. The anterior half of the premaxillary has a longitudinal channel along the side just above the alveolar groove, containing pits for the entrance of nerves to the teeth. Descending to the alveolar surface it will be observed that this element forms the greater portion of the upper jaw. The inner alveolar plate of the premaxillary forms the main part of the arched roof of the upper dental groove. Medially the palatal portion is developed as a long narrow vertical plate that extends downward meeting the same plate of the opposite side mesially for a vertical distance of 12 mm. These narrow alveolar plates posteriorly are separated by the intervention of the anterior extremities of the vomers and pterygoids, which eventually disappear under the premaxillæ.

Basisphenoid (*b.s.*). — In so far as I can ascertain, owing to the damaged condition of this region, the basisphenoid is a heavy subquadrate bone. Posteriorly it articulates with the basioccipital by a deep vertical suture; laterally it is overlapped by the interior processes of the pterygoids; anteriorly the long slender presphenoid is given off. The suture between these bones is not shown nor have I observed it in any of the skulls of *Ichthyosaurus* that are figured. The length of the basisphenoid in specimen No. 603 is about 70 mm.

Presphenoid (*prs.*). — The presphenoid appears as a median anterior prolongation of the basisphenoid. This long trihedral bar gradually tapers to a point as it extends forward. The anterior extremity in No. 603 disappears under the displaced pterygoids. This bone divides the long interpterygoid vacuity into two parts posteriorly.

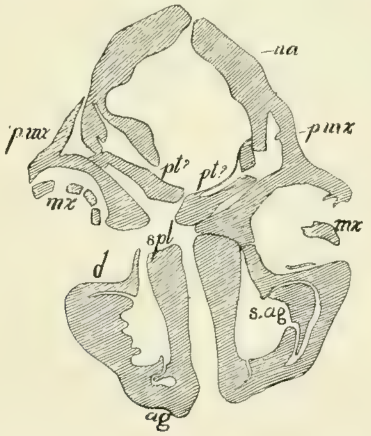
Pterygoid (*pt.*). — The pterygoid is an irregular elongate bone the most conspicuous element of the palatal region. The internal border posteriorly is concave antero-posteriorly and forms the lateral boundary of the interpterygoid vacuity. Posteriorly the inner margin is beveled off to a thin edge which laps over the lateral inferior surfaces of the basisphenoid, and the truncated posterior interior angle probably reached and overlapped the anterior portion of the basioccipital. The posterior end curves slightly upward where the superior surface meets the inferior lateral border of the stapes. Seen from below the posterior border is slightly emarginate, the lateral border posteriorly being deeply excavated. Between this excavation and posterior emargination the pterygoid develops a process that extends outward and downward and laps along the inner inferior one fourth of the quadrate. Anterior to this lateral notch the bone again expands, the lateral extent of which is hidden by the posterior portions of the lower mandible. More anteriorly this element is again excavated by a suture that extends inward and forward, and it is by this suture that the palatines (of modern nomenclature, *transverse bones* of Seeley and Frass, the *ectopterygoid* of Owen), are united with the pterygoids. From this point the latter extend forward and inward, meeting medially, the anterior tapering extremities finally disappearing under and between the vomers. The surfaces of the pterygoids are smooth, both of which dip at a slight angle toward the center of the palate.

Palatines (*pl.*). — The palatines are next in size to the pterygoids of the bones of the palate. They are flat plate-like elements that unite posteriorly with the pterygoids and laterally with the pterygoids and vomers. The outer and anterior extent of these bones cannot be satisfactorily determined from our specimens.

Vomers (*v.*). — These elements are only shown in one specimen, No. 603. Those parts interpreted as vomers are two narrow rod-like bones that begin along the outer anterior margins of the pterygoids. Anteriorly they follow the outline of the skull gradually converging toward one another finally meeting on the median line just before they disappear under the premaxillæ.

There is no evidence of a bone between the vomer and palatine as shown by Frass[31] in *Ichthyosaurus*.

Mandible. — The mandible appears essentially like that of *Ichthyosaurus*. It consists of five and probably six pairs of bones, the dentary, articular, angular, surangular, splenial and coranoid (?) respectively. The element here called splenial is the operculær of Frass.



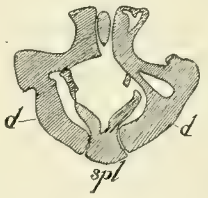


FIG. 1. Cross-section of upper and lower jaws (No. 603), taken at the fracture just above the figure 2 seen in the lateral view of the skull, Plate X. One half natural size. *ag.*, angular; *d.*, dentary; *mx.*, maxillary; *na.*, nasal; *pmx.*, premaxillary; *pt. ?*, pterygoid; *s.ag.*, surangular; *spl.*, splenial.

FIG. 2. Cross-section of the lower jaw of the same taken just anterior to the union of the two rami. One half natural size. *d.*, dentary; *spl.*, splenial.

Dentary (*d.*). —The most anterior and largest of the bones of the lower jaw is the dentary. It forms the greater part of the fore portion of the lower mandible. The posterior extremity ends under the orbit, its posterior suture running obliquely from below the maxillary to a little beyond the posterior end of the symphysis on the lower border. The superior side forms the shallow alveolar channel in which the teeth are supported. (See figs. 1 and 2.) Posteriorly, the thin inner wall of the groove is supported by the quite heavy vertical plate of the splenial, but anteriorly the latter element is supplanted by the higher and thicker inner wall of the dentaries which here exceeds, the outer in height. In specimen No. 878 this inner wall, both at the anterior and posterior parts of the channel, shows some faint vertical ridges, indicative of alveolar compartments. Viewed from below the anterior portion of the dentaries is evenly rounded. Just below the outer alveolar border is a shallow channel into which several vascular foramina open at the anterior end of the jaw.

---

[31] Frass, E., *lit. cit.*, Pl. II., fig. 2.

Splenial (*spl.*).—The splenial in *Baptanodon* as in the other members of this family is a long vertical plate that is applied to and forms the greater portion of the inner surface of the posterior part of the ramus. The anterior portion extends below the dentary a little and is visible from a lateral view of the mandible. Anteriorly it meets its fellow medially where they unite and pass between and under the dentaries. These appear to be ankylosed at the symphysis. (See fig. 2.) Posteriorly the lower margin of the splenial is gradually confined to the inner side and rises obliquely for a considerable distance. This suture at the posterior end of the jaw is obscure and the boundary between the splenial and coranoid (?) cannot be determined, but the latter element probably continues to the end of the ramus, lapping along the inner side of the articular, assisting the angular and surangular in holding that element in position. (See Pl. XI., fig. 2.) On the internal surface, just posterior to the symphysis is an elongated oval foramen that probably represents the "internal mandibular foramen" of the crocodile, though in this case it appears to be wholly enclosed by the splenial while in the crocodile the splenial only forms the anterior border. Posterior to this foramen, from a point on the lower inner side of the mandible, radiating linear impressions extend forward and upward to the posterior border of the vacuity. They would seem to indicate a surface for muscular insertion.

Surangular (*s.ag.*). — Viewed laterally the surangular is a long slightly-bent bone that forms the upper posterior margin of the ramus. On its inner posterior side this bone develops a concave surface (see *sq.*, fig. 3) which with the anterior end of the articular forms the articulating surface for the quadrate. Just in front of this articulating surface is a node-like protuberance which Frass has pointed out as an arrangement to prevent the dislocation of the lower jaws. (See fig. 3.)

The posterior part of the suture between the angular and surangular is not shown by this material, though it is indicated by a dotted line, after the fractures on the rami of No. 878 which were considered as taking the course of these breaks. Anteriorly the surangular gradually tapers to a point which from a lateral view disappears between the dentary and angular just below the nares, although the elements are continued still farther forward on the inside. (See *s.ag.*, fig. 1.) The lateral surface of the posterior end of the ramus in *Baptanodon* is composed of the angular and surangular, the former contributing the greater share. In most of the *Ichthyosaurs* the latter element contributes the greater part.

Angular (*ag.*). — The angular is a long curved bone that forms the lower posterior boundary of the jaw. The anterior end tapers to a point similar to the surangular and disappears between the splenial and dentary just in advance of the anterior end of the surangular. (See Pl. VIII.) The suture between this bone and the splenial posteriorly passes to the inner side. The angular then underlaps the splenial and coranoid (?) and more posteriorly develops an inner plate that encloses the lower part of the articular.

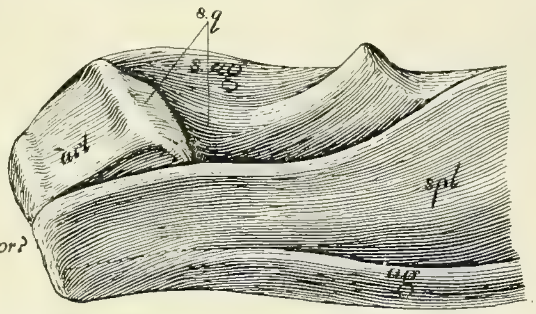


FIG. 3.. Internal view of the posterior end of the left mandibular ramus of *Baptanodon discus* (No. 603). One half natural size. *art.*, articular; *ag.*, angular; *cor.*, coranoid (?); *s.ag.*, surangular; *s.q.*, articulating surface for the quadrate.

Articular (*art.*). — The articular apparently is the least understood of any of the elements composing the Ichthyosaurian jaw. Of all the literature to which I have had access I have yet to find an adequate description of this bone. Fortunately the mandible pertaining to specimen No. 878 has both of these elements preserved *in situ*, while the right articular of No. 603 was found nearly in position but has been detached for purposes of study. It is this element upon which this detailed description is based.

As in most reptiles the articular is placed far back in the ramus. In *Baptanodon* it is held in position by the enclosing walls of the angular, surangular and coranoid (?). The angular entirely encloses the lower portion curving up on the inner side, developing even more of an inner portion than is found in the Crocodile. Viewed superiorly the articular is a short solid subrectangular bone (see figs. 4 and 5.) The upper surface is smooth and gently convex transversely, quite flat anteroposteriorly with the exception of an elevated transverse ridge at either end. Posteriorly the end is subtriangular in form the longer side looking downward and outward. This end is somewhat convex from above downward, presenting a slightly roughened surface. The outer lateral surface of this bone is concave from above downward (see fig. 5) and roughened for ligamentous attachment to the surrounding bones. The inner surface is irregularly concave and roughened down to the inferior wedge-like edge. Anteriorly the end resembles that of the posterior view though somewhat dished from above downward, and more compressed transversely. It was this end of the articular with the surangular that formed the concave articulating surface (*sq.*), for the quadrate. There is no anterior process or elongation of this bone and in this respect the articular of *Baptanodon* is much shorter than the corresponding element in the Crocodilia.

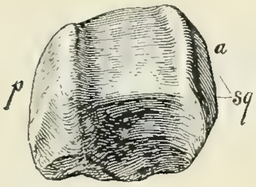


FIG. 4. Internal view of left articular of *Baptanodon discus* (No. 603). One half natural size. *a.*, anterior end; *p.*, posterior end; *sq.*, articulating surface for quadrate.

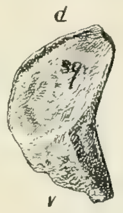


FIG. 5. Anterior view of same bone. One half natural size. *d.*, dorsal surface; *s.q.*, articulating surface for quadrate; *v.*, ventral surface.

In the posterior position of the articular the manner by which it is retained in the jaw and the part it takes in forming the articulation for the quadrate it is most nearly approached by the articular of *Chelone midas*.

I have observed several figures of the lower jaw of *Ichthyosaurus* which show the articular as a small triangular bone at the posterior end of the ramus lying between the surangular above and the angular below and visible from a side view. In the specimens considered here the articular cannot be seen from a lateral view. The coranoid (?) apparently overlapped the inner margin above the angular.

Coranoid (*cor.*). — Of our knowledge of the extent and nature of the coranoid in *Baptanodon* little can be said at this time. In our specimens it appears as a comparatively thin plate that extends along the inner side of the posterior end of the ramus, lapping over the lower border of the articular, thus assisting the angular and surangular in holding that element in position. Nothing is known of its extent anteriorly.

I am pleased to acknowledge my indebtedness to Dr. J. C. Merriam for the identification of this element in the material under discussion. On his return from Europe last year he examined the skulls and kindly gave me the benefit of his observations.

Dentition. — The presence of teeth in the American species has long been suspected by many paleontologists, but until recently[32] there has been no positive evidence of their existence. The shallow dental grooves combined with the reduced size and undoubtedly loose attachments of the teeth, will fully account for their absence in previously discovered specimens. The English form *Ophthalmosaurus icenicus* shows about the same peculiarity in the retention of the teeth. Baur[33] has observed small teeth at the end of the jaws of the (Baptanodontidæ) *Ophthalmosaurus* contained in the private collection of Mr. Leeds in Peterborough, England. Lydekker[34] also speaks of alveoli being present at the end of the jaw in this genus, although the groove is known to extend posteriorly.

---

[32] Gilmore, C. W., "Discovery of Teeth in Baptanodon, an Ichthyosaurian from the Jurassic of Wyoming," *Science*, N. S., Vol. XVI., No. 414, pp. 913–914, Dec., 1902.

In the jaws of No. 878, although the alveolar channels are better preserved than in specimen No. 603, there was not even a fragment of a tooth recovered, but we have evidence of their existence at one time in the faint alveolar partitions preserved on the inner wall of the right dental groove. (See Pl. VIII.)

As suggested in a preliminary paper in *Science* the final exhumation of the jaws of No. 603 revealed more teeth, nine in all, six of which were in the groove of the upper jaw, the remaining three being attached by matrix to the alveolar surface of the lower mandible. With but one exception all of the teeth were lying prone upon the surfaces of the grooves.

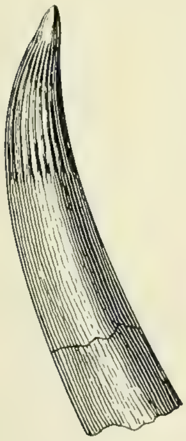


FIG. 6. Posterior tooth of *Baptanodon discus* (No. 603). Twice natural size. The transverse fracture represents the point at which the cross section was drawn.

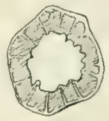


FIG. 7. Cross section of the same tooth (No. 603). Nearly twice natural size.

The largest and best preserved tooth found was cemented to the lower jaw by the matrix just anterior to the forward extremity of the left maxillary. The tooth as preserved (see fig. 6) measures 29 mm. in length, and undoubtedly represents the teeth of the posterior part of the series. The base (see fig. 7) is somewhat angular in cross section, but as the tooth rises it becomes more rounded ending in a circular subacute apex. There is no swelling of the base as may be observed in the teeth of many of the *Ichthyosaurs*. A little more than the upper third is covered with enamel which is impressed with fine longitudinal striæ, between which are intervening depressions. These grooves begin quite abruptly at the base of the enameled surface and extend upward, gradually subsiding before reaching the apex which is smooth. A cross section near the mid portion of the cement covered base shows the tooth to have a somewhat flattened periphery at either end of the line of its greatest diameter. Considering these surfaces as the contact between the tooth and the outer and inner walls of the dentary groove, the tooth would curve in slightly. But it is hard to understand how the shallow and widely separated walls of this groove could ever have been in apposition with the teeth it bore. The teeth of the median part of the snout were more slender, but otherwise appear to be identical with the tooth described above. The two most anterior found at a point just posterior to the tip of the rostrum were small, more cone-like, but otherwise similar to those preserved posteriorly. It would appear from the evidence before me that: *Baptanodon was well provided with comparatively small, somewhat slender but functional teeth that extended along the full length of the jaw; the most anterior ones being much reduced.*

---

[33] Baur, *lit. cit.*

[34] Lydekker, R., "Catalogue of Fossil Reptilia and Amphibia in the British Museum."

The teeth of *B. discus* differ from the one tooth known of *B. natans* in the perfectly smooth enameled surface of the latter.

Thyrohyal (*th.*). — Lying parallel to the posterior part of the right mandibular ramus of No. 878 was a subcompressed rib-like bone which I have considered the *thyrohyal* as described by Owen. There was no evidence of the corresponding bone of the opposite side. Both ends are expanded, more especially the posterior which is almost twice the width of the anterior. Pl. XI., fig. 1 (*th.*), gives the position of the element as retained in the matrix.

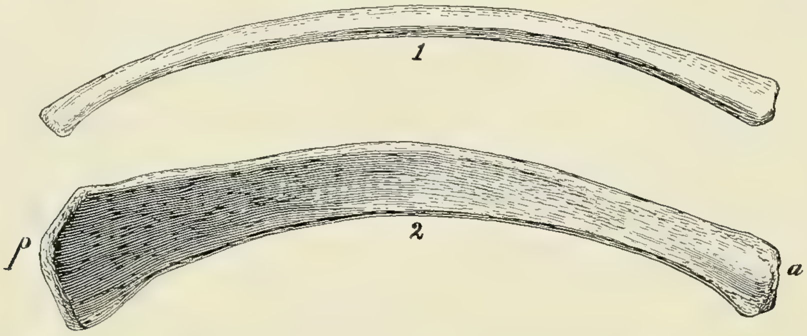


FIG. 8. Right thyrohyal of *Baptanodon discus* (No. 878). One half natural size. 1, view of the inferior border; 2, lateral view; *a.*, anterior end; *p.*, posterior end.

An inspection of fig. 8 (1 and 2) shows this element as being curved from end to end both vertically and laterally.

MEASUREMENTS.

No. 878.	Greatest length of thyrohyal	191 mm.
" 878.	" width of posterior end	35 "
" 878.	" " anterior "	20 "

THE VERTEBRAL COLUMN.

The material under discussion is not well adapted for a systematic study of the several regions of the vertebral column, and although vertebræ are preserved from the different regions of the back bone, the vertebral series is imperfect in all of the skeletons in this museum. The description of this part of the axial skeleton will be supplemented somewhat by the more complete vertebral series in the collections of the University of Wyoming.

With skeleton No. 603 there are thirty or more vertebræ in various degrees of preservation, but there are none arranged serially. However, every part of the column is represented.

Specimen No. 878 has a series of twenty-one vertebræ extending from the atlas backward. (See Pl. VII.) The first fifteen are in a fair state of preservation but the remaining six are very imperfect. The spinous processes are only preserved in a few instances.

No. 919 which is a much larger individual has a series of ten cervicals commencing with the atlas, a second series of eleven from the anterior dorsal region posterior to the point where the diapophyses become distinct from the neurapophysial articular surface; a third section of eleven posterior dorsals commencing just posterior to the first vertebra having the diapophysis and parapophysis united to form a single node-like articulation. The fourth and last section contains parts of twelve anterior caudals, these show the rapid decrease in the size of the centra posteriorly as previously pointed out by Knight.[35]

The centra in all regions anterior to the extreme caudals are deeply biconcave. These concave surfaces, with the exception of the anterior face of the atlas, begin close to the periphery and slope in rapidly but evenly to the center. In this respect *Baptanodon* may be distinguished from *O. icenicus,* as Lydekker[36] observes of the vertebræ referred to the latter genus. "The cervical region with the cupping of the anterior face of the centrum confined to the central portion, and surrounded by a flattened periphery." There are some isolated centra of this character in the collections of the Yale Museum, labelled as coming from the *Baptanodon Beds* of the Rocky Mountains. From this slight evidence it would appear as though the genus *Ophthalmosaurus* may also occur in this country.

The upper arches in this genus as in all previously described Ichthyosaurians are free from the centra and were united to them by synchondrosis. The centra are always short antero-posteriorly as compared with their breadth and height.

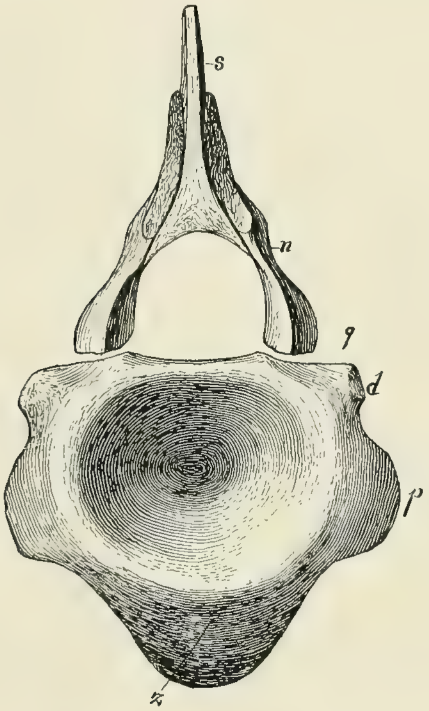
Atlas and axis (*at. and ax.*). — In *Baptanodon* as in nearly all adult members of the *Ichthyosauria,* the centra of the atlas and axis are completely fused, so much so that one would hardly suspect the existence of two vertebræ if it were not for the presence of the two sets of arches upon their dorsal surfaces (see figs. 10 and 26). These vertebræ are represented in all three specimens, Nos. 603, 878 and 919. Those of No. 878 are in the best state of preservation and are the elements from which the text figures have been drawn. Though not found in position (see Pl. VII.) they are readily distinguished from the succeeding vertebræ by their more modified centra and by their dorsal and transverse processes.

---

[35] Knight, W. C., "Some Notes on the Genus Baptanodon, with a Description of a New Species," *Am. Jour. of Sci.* (4), Vol. XV., 1903.

[36] Lydekker, *lit. cit.*

Seen anteriorly (see fig. 9) the centrum of the atlas is pentagonal in form, wider than deep and considerably contracted inferiorly. The concavity for the reception of the occipital condyle instead of sloping from the outer margin to the center as in the centra that follow, has a narrow, flattened periphery, which is much enlarged laterally and inferiorly. The cup of the centrum descends evenly, perhaps more sharply, from the superior margin down to the center. The inferior surface presents a slightly rounded subtriangular face which looks downward and forward, its inferior extent reaching nearly to the middle of the coalesced centra. If present it was with this face or apophysis that the first hypophysis or intercentrum articulated. The superior lateral surfaces are quite extensive and curve backward to form the para- and diapophyses. The dorsal surface is about equally divided between the



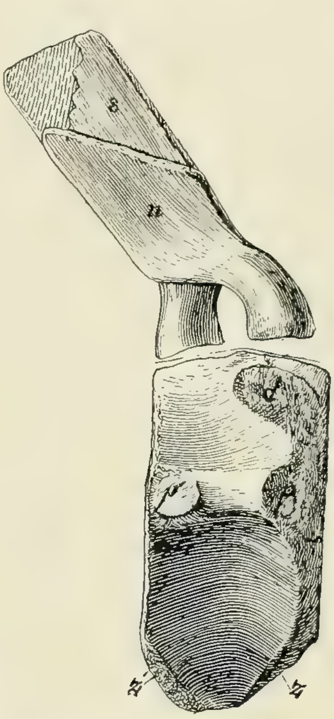


FIG. 9. Anterior view of atlas and axis of *Baptanodon discus* (No. 878). One half natural size. *d.*, diapophysis; *n.*, paired neural arch of atlas; *s.*, spinous process of axis; *z.*, apophysis with which the first intercentrum articulated.

FIG. 10. Lateral view of atlas and axis of *Baptanodon discus* (No. 878). One half natural size. *d.*, diapophysis of the atlas; *n.*, paired neural arch of atlas; *p.*, and *p.'*, parapophysis of the atlas and axis respectively; *s.*, spine of the axis; *z.*, apophysis of the atlas; *z.'*, apophysis of the axis.

neural canal and the surfaces for the attachment of the pedicles of the neural arch, the two surfaces being separated by narrow antero-posterior ridges.

The lateral surface of the combined centra (see fig. 10) is somewhat concave antero-posteriorly. Superiorly the neurapophysial surface extends outward and coalesces with the heavy articular diapophysis. There is no indication of a diapophysial surface on the axis such as is seen in the axis of *B. marshi* (fig. 26), or the axis of *I. longifrons*, Owen. Just below the diapophysis and separated from it by a non-articular tract is an antero-posterior ridge at either end of which arise articular prominences which represent the parapophysis of the atlas and axis respectively. The parapophysis of the atlas (*p.*) being the larger of the two. The round tubercle like parapophysis (*p.'*) of the axis is placed well posterior on the side of that vertebra. The lateral margin below the parapophysis is concave antero-posteriorly even down to the furthermost extent of the inferior subtriangular part of the centra. I have examined the coalesced centra pertaining to six different Ichthyosaurian skeletons from the Jurassic of North America and have yet to find a trace of the suture uniting the atlas and axis.

Posteriorly (see fig. 11) the centrum of the axis is deeply concave, the surface) slopes in gradually from the outer margin for half of the radius, thence more sharply to the center. Inferiorly the lower surface is produced into a subtriangular face which looks downward and backward, at a somewhat sharper angle (see fig. 10 than the apophysis of the atlas. This would be the articulation for the third intercentrum if that bone still exists as a separate element in this form. The axis of *B. marshi*, shows no such face, though the apophysis of the atlas appears to still be present. The axes of both No. 603 and 919 appear to be identical with that of No. 878. In these forms it would seem that at least two intercentra exist as separate elements while the one between the atlas and axis has become completely anchylosed to the centra. I have examined the atlas and axis of *B. marshi* (see fig. 26) and find here a still greater reduction in the number of

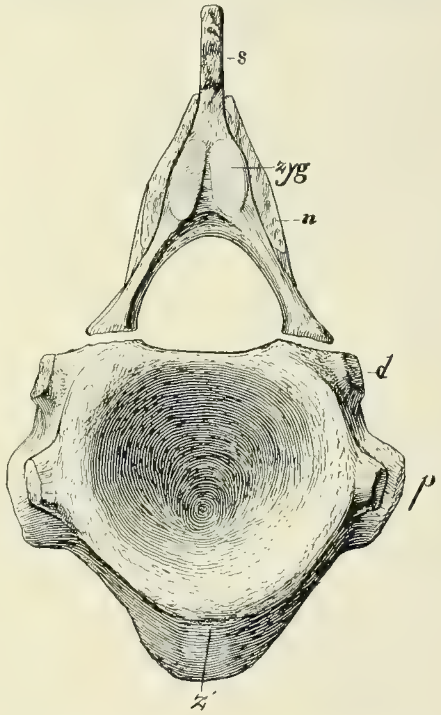
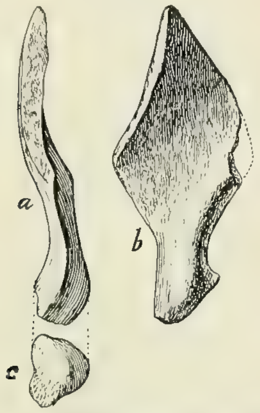
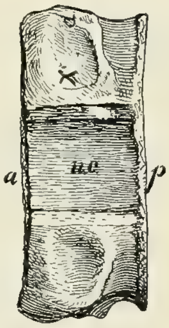


FIG. 11. Posterior view of the atlas and axis of *Baptanodon discus* (No. 878). One half natural size. *d.*, diapophysis of the atlas; *n.*, neural arch of the atlas; *p.*, parapophysis of atlas; *s.*, spine of the axis; *zyg.*, posterior zygapophysis of the axis; *z.'*, apophysis for third intercentrum.

the intercentra. There could not have been more than one retained and it may be possible that all have disappeared. This indicates a higher degree of specialization than has hitherto been found to exist among the Ichthyopterygia. The Triassic form *Shastasaurus*,[37] Merriam has five intercentra while in *Ichthyosaurus* there are but three.

The paired neural arch is the only process supported by the atlas. They extend upward and backward overlapping the lateral basal portion of the spine of the axis and never uniting to form a spine. The left half of this arch was found displaced though in an excellent state of preservation. Viewed from the side (fig. 12, *b*), it is an irregular spear-shaped compressed bone that articulated with the centrum by an expanded subtriangular articular end (fig. 12, *c*). An anterior view (fig. 12, *a*) shows the sinuous curves made necessary for it to fit closely to the process of the axis. The function of these bones appears to be the same as the corresponding elements of *I. longifrons* as described by Owen, which they resemble somewhat in shape and position. This paired neural arch does not develop zygapophyses. The pedicels of the axis as they rise from the surface of the centrum converge and meet above the neural canal to form a well-developed neural spine, the first of the vertebral series. There are no indications of prezygapophyses on the spine of the axis belonging to No. 878, though the process of *B. marshi* shows such articulating surfaces. The posterior portion of the spine is broken away so that its extent antero-posteriorly cannot be determined accurately from our specimens, and it would appear after an





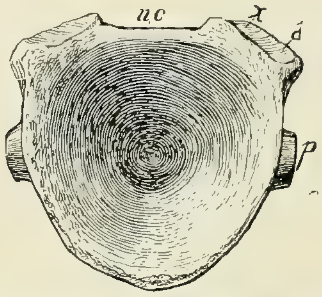


FIG. 12. Left half of paired neural arch of atlas of *Baptanodon discus* (No. 878). One half natural size. *a*, seen anteriorly ; *b*, seen laterally ; *c*, view of distal or articular end.

FIG. 13. Superior view of an anterior cervical of *Baptanodon discus* (No. 603). One half natural size. *a*, anterior *d* and *x* the combined dia- and neurapophysial surfaces ; *n.c.*, neural canal ; *p*, posterior.

FIG. 14. Anterior view of anterior cervical of *Baptanodon discus* (No. 603). One half natural size. *d* and *x*, the coalesced diapophysis and neurapophysial surfaces ; *n.c.*, neural canal ; *p*, parapophysis.

---

[37] Merriam, J. C., "Triassic Ichthyopterygia from California and Nevada," Univ. of Cal. Pub., Vol. 3, No. 4, p. 75.

examination of the axis of *B. marshi* that the restored spine in fig. 10 is too narrow antero-posteriorly.

Vertebræ Posterior to the Axis. — The succeeding cervicals are very similar in their general form which perhaps is best described as "shield shaped." Fig. 14 is a good example of the cervical centrum and the description given here may be considered typical of the vertebræ of this region.

On the median superior surface is the smooth tract forming the basal boundary of the neural canal (see fig. 13) on either side separated by slight antero-posterior ridges are the shallow roughened neurapophysial surfaces for the attachment of the pads of cartilage upon which the pedicels of the neural arch rested.

This roughened surface is placed largely on the anterior half of the cervical and extends outward and downward becoming confluent with the diapophysis (see fig. 14). The parapophyses are node-like projections placed half way down and on the anterior margin of the centrum, being separated from the diapophyses by a concave longitudinal depression. The position of these two processes remains unchanged as far back at least as the fifteenth vertebræ, as will be seen in Pl. VII.

The anterior vertebræ are broader than high and gradually increase in length posteriorly. From the splendid series of forty-one precaudal vertebræ pertaining to the type of *B. marshi*, Dr. Knight has observed that the maximum length is reached in the nineteenth from the skull.

Continuing back in the column (see fig. 15) it will be observed that the centra remain about the same height but the transverse extent becomes considerably greater, also the articular surfaces of the diapophyses which are confluent with the neurapophysial surfaces in the cervical region become separated. In *Ichthyosaurus* this separation takes place on either the fourteenth or fifteenth vertebra. Dr. Merriam has shown that in one species of *Shastasaurus* it does not occur until the thirty-fifth or later. The point at which this transition is brought about in *Baptanodon* cannot be determined from the specimens under discussion, although we have evidence that they do not separate until the sixteenth or later.[38] (See Plate VII.)

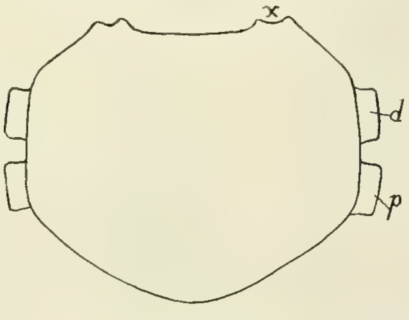
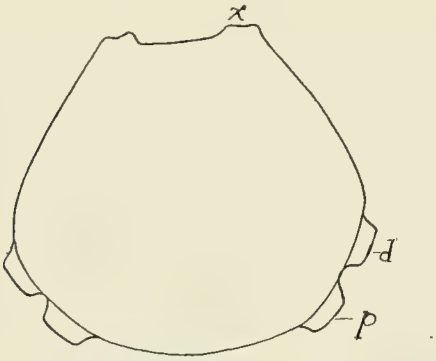


FIG. 15. Cross section of an anterior dorsal centrum of *Baptanodon discus* (No. 603). One half natural size. *d*, diapophysis; *p*, parapophys; *x*, neurapophysial surface.

---

[38] In the *Am. Jour. Sci.*, Vol. 50, 1895, Marsh figures a vertebra of *Baptanodon natans*, designated as a cervical, The position of the dia- and parapophyses half way down on the side of the centrum at once shows this vertebra as pertaining to the region posterior to the neck. This figure was published a second time in his U. S. G. S. Monograph of the Vertebrate Fossils of the Denver Basin in 1897.

From the cervicals back through the dorsal region the breadth remains greater than the height but the shield-shaped form of the cervical centra gradually changes to what has been called "pear shaped" (see figs. 16 and 17), in the regions here considered as middle and posterior dorsals, and this form gradually assumes the compressed elliptical contour seen in the caudals (see fig. 19).



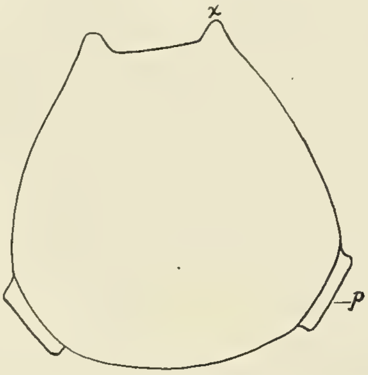


FIG. 16. Cross-section of a dorsal centrum of *Baptanodon discus* (No. 603). One half natural size. *d*, diapophysis; *p*, parapophysis; *x*, neurapophysial surface.

FIG. 17. Cross-section of posterior dorsal or anterior caudal centrum of *Baptanodon discus* (No. 603). One half natural size. *p*, (?) parapophysis; *x*, neurapophysial surface.

The change in form of the centra brings a corresponding transition of the dia- and parapophyses. These processes gradually move down the side of the centra, until finally only one oblique process remains on the extreme lower side of the centrum. This type probably represents the posterior dorsal region (see fig. 17).

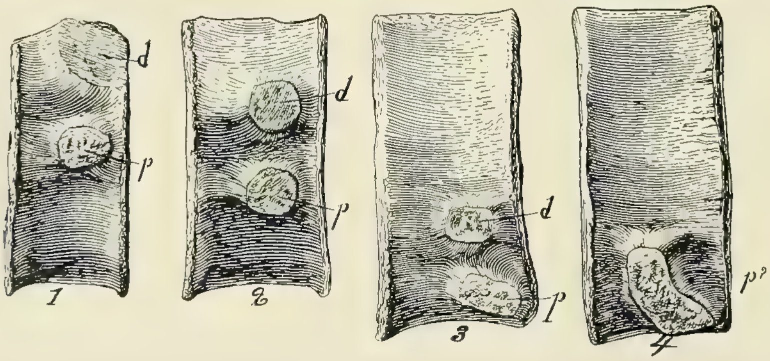


FIG. 18. Lateral view of centra from different regions of *Baptanodon discus* (No. 603). One half natural size. 1, anterior cervical; 2, anterior dorsal; 3, dorsal; 4, posterior dorsal or anterior caudal; *d*, diapophysis; *p*, parapophysis.

In *Ichthyosaurus* Owen described the reduction to a single facet as a union of the two 'pophyses. He thought the diapophysis dropped more rapidly than the parapophysis, thus meeting the latter with which it united to form the single oblique process.

The evidence to which I have had access is not conclusive but it has suggested to me that in *Baptanodon* this is not a union of the two but a development of the parapophyses with a consequent reduction and final passing away of the diapophyses. (Compare 1, 2, 3, 4, fig. 18.) It will be noticed in the cervical (1) region that the diapophyses presents the more robust articular surface of the two; the anterior dorsal (2) shows the two facets nearly equal; the median dorsal (3) indicates an increase in size of the parapophysis with a corresponding decrease of the diapophysis. It will be observed that in all three regions the distance between the facets remains about constant.

In the Triassic genus *Shastasaurus* Dr. Merriam has shown that the parapophyses become obsolete in the anterior dorsal region with a consequent increase in the size of the diapophyses.

The single process in *Baptanodon* gradually decreases in size posteriorly and finally fades away at some point in the caudal region as is shown by fig. 19. Owen has shown that this single process in *I. communis* disappears on the eightieth vertebra and it is at this point that the downward bend or depression of the tail takes place.

Professor Knight has added some important information to our knowledge of the tail of the American form as follows: "In specimen 'T' in the same collection (University of Wyoming) there are forty-six consecutive caudal vertebræ. These are of the usual ichthyosaurian type and represent an animal that had an extremely long and slender tail. The reduction in the size of the vertebræ occurs very near the body and within a distance of a few inches, the vertebræ decrease in diameter over one half. The vertebræ in the area of reduction have reduced margins,[39] in fact in two of them the articulation nearly meets upon the side of the centrum. * * * Although caudal vertebræ from at least a half dozen different animals have been examined, no trace of chevrons has been observed, and the vertebræ lack chevron facets."

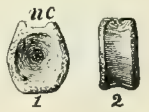


FIG. 19. 1 and 2, end and lateral views of an extreme caudal of *Baptanodon discus*. (No. 603). One half natural size. *nc*, neural canal.

On the anterior vertebræ the neural arches are held together by well developed zygapophyses. The anterior arches have paired zygapophysial facets which unite to form a single median one at some point between the sixth and ninth cervicals. This information is derived from the cervical region of No. 878. The zygapophysial facets have their surfaces roughened indicating as shown previously by Dr. Merriam in the genus *Shastasaurus*, the presence of considerable cartilage.

A number of the anterior cervicals of No. 878 (see Pl. VII.) have the arches and spines preserved nearly in place, the anterior zygapophyses of these look upward and slightly inward, the planes of which if continued to intersection would meet at an angle of 160° to 170°. The posterior zygapophyses look downward and somewhat outward, being separated by a slight vertical depression.

---

[39] It occurs to me that these vertebræ with reduced margins may represent the point of divergence of the vertebral column into the lower lobe of the caudal fin.

The neural arches as they rise from the centra are slightly inclined backward. This inclination is continued in the spinous process at a still greater angle. The spines of the anterior vertebræ are greatly compressed laterally, being flattened into a subquadrate plate of bone that is somewhat thickened above. Of the spinous processes of the posterior vertebræ nothing of importance is shown by the material under discussion, though the articular bases of the pedicels must undergo modifications corresponding to those that take place on the dorsal surface of the centra of the several regions. Anteriorly the base is subtriangular in form and somewhat protuberant, but upon the centra where the separation of the diapophysis and neurapophysial surfaces takes place the articular end becomes long and narrow, and rests upon corresponding ridges which rise from the dorsal surface of the centrum. (See fig. 17, *x*.)

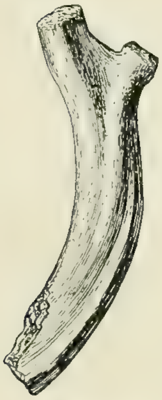


Fig. 20. Posterior view of a right dorsal (?) rib of *Baptanodon discus* (No. 603). One half natural size.

Ribs. — Though there are numerous parts of ribs preserved with the different skeletons no complete ribs have been found. Those pieces lying on either side of the anterior vertebra of No. 878 (see Pl. VII.) show the ribs of this region to have been very long and slender. On the left side of the column (r') is about 725 mm. long although both ends are wanting. This evidence appears to indicate a very deep body cavity anteriorly. Corresponding to the form of the anterior vertebræ the ribs have a distinct tuberculum and capitulum. The latter probably as in the other groups of the Ichthyopterygia disappears in the posterior dorsal region. As yet the abdominal splint-ribs so numerous in *Ichthyosaurus* have not been observed in this genus.

Pectoral Arch. — Plate XII., Figs. 1, 2 and 3.

The pectoral girdle of *Baptanodon* is represented in two specimens, Nos. 878 and 919, the former having the most complete arch yet discovered of this genus. Fig. 21 shows the inferior view of the elements as they were retained in the matrix. The girdle pertaining to No. 919 though incomplete has been entirely removed from the matrix and it gives us a good idea of the anterior and superior aspects of this region. (See Pl. XII., figs. 1 and 2.) As mentioned previously this specimen may prove to belong to a different species when more complete material is known.

It will be observed in fig. 21, that with the exception of the clavicles and interclavicle the other elements have been retained in their mutual relations and establishes for all time the relative position of the scapulæ and coracoids of this genus. The position of the clavicles and interclavicle can be determined with a fair degree of accuracy. An examination of the roughened surfaces (*x* and *x*), for ligamentous attachment on the anterior borders of the scapulæ shown best in Pl. XII., figs. 1 and 2, No. 919 evidently indicates the place of attachment for the clavicles. The firmly united clavicles evidently curved up along the anterior borders of the scapulæ and coracoids, being attached to the former by ligaments at *x* and *x*, to the latter by the interclavicle, which fits into a groove on the posterior median side of the clavicles and extends back until its upper excavated surface laps under the anterior median union of the coracoids, the position in extant Lizards, thus forming a brace between the two parts of the girdle. In both specimens the girdle is formed essentially in the same manner as in *Ichthyosaurus*.

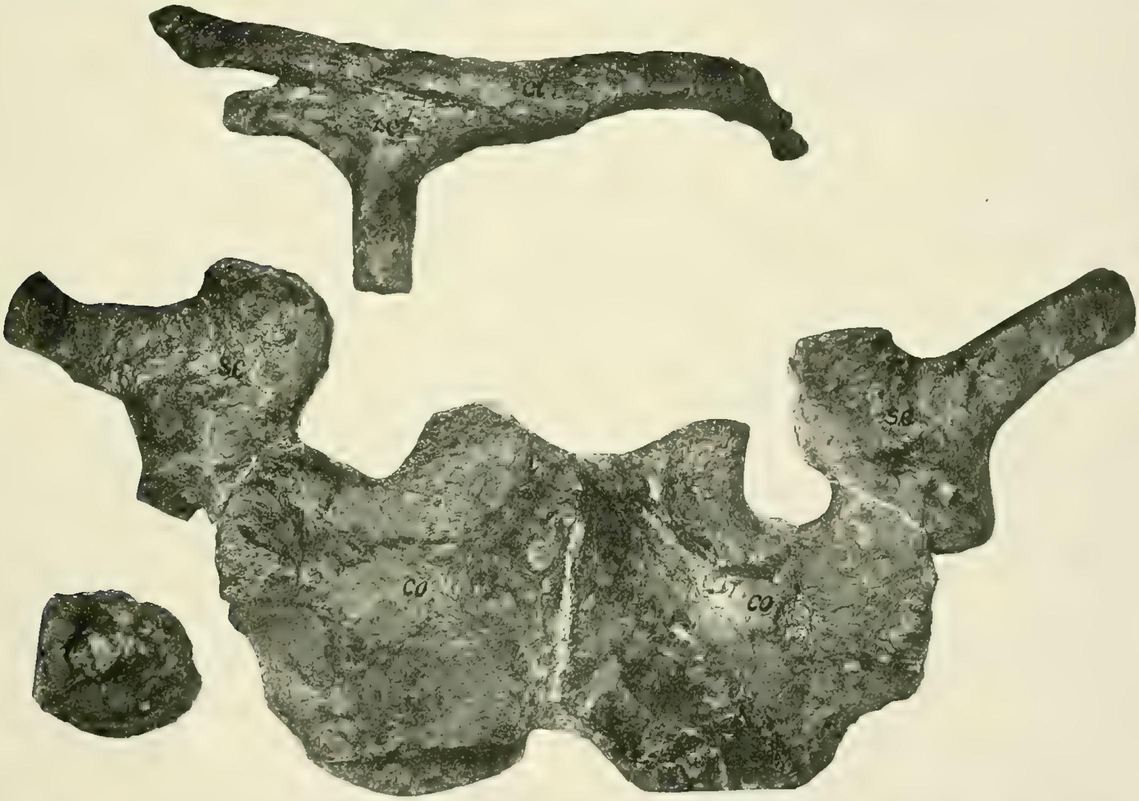


FIG. 21. Ventral view of the pectoral girdle, as found in the matrix. *Baptanodon discus* (No. 878). One fifth natural size. *cl*, clavicle; *co*, coracoid; *h*, humerus; *i.cl*, interclavicle, *sc*, scapula.

Dr. Knight's observation that: "There was no evidence of an interclavicle, and the peculiar union of the coracoids precludes an interclavicle of the regular Ichthyosaurian type. In consequence the interclavicle in Baptanodon must be considered rudimentary or wanting," must have been based upon a comparison of the coracoids of *B. marshi* with those figures of *Ichthyosaurus* which show the interclavicle as lying between these elements anteriorly. The portion of a girdle figured by him appears to be identical in form with the arches under discussion, one of which, No. 878, has a well developed interclavicle making it appear that Knight was mistaken in his interpretation of this region.

Coracoid (*co.*). — The coracoids are broad subquadrangular bones that join one another medially by large elliptical facets. These facets are roughened and were evidently united by a heavy pad of cartilage, the width of which is best shown in Pl. XII., figs. 1 and 2.

The internal or superior surfaces (Pl. XII., fig. 2), are flattened, though both elements are gently inclined toward the median line. The external or inferior surfaces are concave transversely and convex antero-posteriorly. The lateral borders are especially thickened forming a heavy articular face for the scapulæ and humeri. This outer articular end is divided into two unequal faces meeting in an obtuse angle. The more anterior and smaller one of the two is for the scapula, and looks outward, forward and obliquely upward. The larger and posterior surface forms the greater part of the glenoid cavity. It is very slightly convex from above downward and covered with tubercle-like eminences indicative of a heavy pad of cartilage. This articular end is supported by a broad neck formed by a deep notch on the anterior margin and a slight emargination on the postero-lateral border of the coracoid. This anterior notch Seeley suggests, probably corresponds to the foramen found in the coracoids of the Dinosaurs.

The anterior border from the inner notch thickens rapidly as it recedes posteriorly to form the intercoracoidal facet (see Pl. XII., fig. 1). The posterior part is compressed to a thin plate, the border being rounded from the inner angle of the emargination to the median union of the two elements.

The coracoids resemble those of the long-snouted species or Latipinnate form of Ichthyosaurs of which *I. tenurostris* is a good example.

MEASUREMENTS.[40]

No. 878.	Greatest length of coracoid antero-posteriorly	253 mm.
" 878.	" width " " transversely	208 "
" 919.	" " " " "	200 "
" 878.	" " " girdle end to end of scapulæ	770 "

Scapula (*sc.*). — The scapula is a moderately long bone, the upper half being narrow with nearly parallel sides, the lower or articular portion is broadly expanded antero-posteriorly and is especially thickened on the posterior margins where it enters into the formation of the glenoid cavity. The articulating face for the coracoid joins this border at an obtuse angle.

---

[40] Measurements given of No. 878 are made from the right element, which appears to be the least distorted.

The scapula extends outward, upward and forward, not backward as Seeley suspected in his original description of the type of *Ophthalmosaurus.* Both arches before me have the scapulæ retained in their natural relations to the coracoids and their position may be considered as absolutely determined. Viewed longitudinally the inner surface of the scapula is slightly concave, as it curves up to lap over the side of the ribs. On the upper free end the inner surface is quite flat, distally the articulating end is concave antero-posteriorly. The anterior border above is gently rounded but as it approaches the articular end it widens into a flattened oblique surface (x) that looks forward and upward. (See Pl. XII., figs. 1 and 2.)

Seeley[41] regarded a part of this border as the acromion process. The oblique surface mentioned above is roughened and I have interpreted it as being the place of attachment for either the ligaments or cartilage which held the clavicles in position. The position of these elements is beautifully shown by a specimen of *I. quadriscissus,* No. 6293, in the Stutgarter collection of which Frass[42] gives a figure.

The scapulæ of our specimens are not notched to fit over the articulating surfaces of the coracoids as figured by Knight but unite by nearly straight articulating faces. An examination of Dr. Knight's specimen, the type of *B. marshi,* convinces me that the articular ends of the scapulæ of that species are not different than those of *B. discus,* but in the former case were crushed so that their true shape and relations could not be accurately determined. The lower surface of the scapula is convex from end to end. Antero-posteriorly the free end is gently convex, but somewhat concave at the expanded articular end. Between the marginal "acromion process" and the articulation with the coracoid the internal border is especially compressed and remains free.

Seeley has best described the humeral articulating border as follows: "The humeral articulation is an expanded triangular thickening of the bone, extending posterior to what would otherwise be an extension of the parallel sides of the free or distal end."

MEASUREMENTS.

No. 878.	Greatest width of free end of scapula.	55 mm.
" 878.	" " " articulating "	173 "
" 878.	" length " scapula	248 "

Clavicles (*cl.*). — So far as I am able to learn specimen No. 878 is the first *Ich-*

---

[41] Seeley, H. G., *Quart. Jour. Geol. Soc. of London,* Vol. XXX., pp. 696–707, 1874.

[42] Frass, E., *lit. cit.,* Plate IV., fig. 2.

thyosaurian from the Jurassic of America to have the clavicle and interclavicle bones preserved. The position of these elements as retained in the matrix is well shown in fig. 21. It will be observed that the upper extremity of the right clavicle as well as the right transverse end of the interclavicle are wanting.

Viewed anteriorly if complete the anchylosed clavicles are bow-shaped, widest at the middle, gradually narrowing as they turn up along the anterior borders of the scapulæ. The ends must have been directed upward, outward and backward to the extent that either clavicle would be opposed to the oblique roughened surface[43] on the inner anterior borders of the scapulæ which look forward and upward. The outer or upper third must have been free from the scapula though lying parallel with the free end of that element.

The left clavicle which is quite complete at its upper end is subcircular in cross-section. The broken end of the right clavicle is somewhat angular in cross-section. On the median posterior side of the blended clavicles is a deep longitudinal groove for the reception of the transverse portion of the interclavicle. The latter is shown in fig. 21 a little removed to the left from its normal place in the clavicular girdle.

Professor H. G. Seeley has pointed out four different ways by which the clavicles unite in *Ichthyosaurus.* 1, clavicles anchylosed or connate; 2, clavicles meeting in the median line; 3, clavicles not meeting but joining by squamous union with the extremities of the interclavicle; 4, clavicles united by a long squamous suture. He adds a fifth in *Ophthalmosaurus,* 5, clavicles united medially by an interlacing suture. He considered these differences of generic value, and the fifth was one of the important characters upon which he based the genus *Ophthalmosaurus.*

A careful comparison of Seeley's figures and description of the clavicles of *Ophthalmosaurus* with those of specimen No. 878 shows many similarities. Although the presence of a suture and the interclavicle wedged in between the ends of the clavicles in the former seems to indicate a distinct difference from the anchylosed clavicles of *Baptanodon* which show no evidence whatever of a suture at the median junction.

Interclavicle (*i.cl.*). — With the exception of the right end of the transverse bar (see fig. 21), this element appears to be complete. It is of the usual "T"-shaped form, though possibly not quite so robust as observed in many members of the genus *Ichthyosaurus.*

The inferior surface of the posterior stem is rounded transversely. The parallel borders of this part as they extend forward diverge rapidly forming a wide triangular plate whose outer apices are produced to form the ends of the transverse bar. This transverse portion lies in a groove on the posterior side of the clavicles and when in position only the stem could be seen from an inferior view of the girdle. (See Pl. XII., fig. 3.) An examination of fig. 21 shows the interclavicle slightly removed to the left from its natural position in the groove of the clavicles.

---

[43] Cuvier in "Ossemens Fossiles" as early as 1824 points out that the scapula of *Ichthyosaurus* has at its anterior edge a prominence which supports the extremity of the clavicle.

The upper posterior side of the stem is gently concave from side to side, indicating that it probably underlapped the median ventral surfaces of the coracoids, thus giving support to the forward part of the arch.

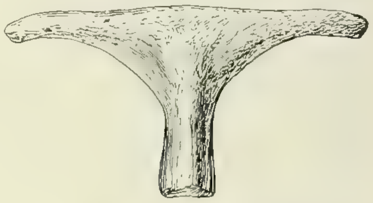


FIG. 22. Inferior view of interclavicle of *Baptanodon discus* (No. 878). One fifth natural size.

Nothing is known of the pelvic girdle at this time.

Anterior Limbs.—Professor Marsh briefly described the fore paddle (probably pertaining to specimen No. 1958) of *Baptanodon* as follows: "In the fore paddle the humerus alone is differentiated. Below this the bones of the forearm, the carpals, metacarpals and phalanges are essentially rounded free disks implanted in the primitive cartilage. The radius may perhaps be regarded as a partial exception, as its free margin is nearly straight and somewhat thinner than the remaining border. There are three bones of nearly equal size in the first row below the humerus. The radius may be identified with certainty by its position. The next bone evidently corresponds to the intermedium[44] and the third or outer one, to the ulna. In the succeeding row there are four subcircular bones, and five in the next series. These represent the carpals. There are six metacarpals, and also six well-developed digits, each composed of numerous phalanges, which are free and nearly circular in form."

Knight has given additional information of the paddle bones in the following lines: "The carpals, metacarpals and phalanges are compressed grooved cylinders the most of which have slightly concave surfaces. The grooves are ornamented with tuberosities for musular attachment. Along the margins of the limb the cylinders have their exterior borders reduced to quite thin edges. Anyone finding the limb of a *Baptanodon* for the first time scattered about in the field would surely try to fit the ventral and dorsal surfaces of the metacarpals in trying to construct a digit."

There is nothing to be added to this description by our material which consists of the proximal end of a humerus (see fig. 21, *h*), and a few miscellaneous paddle bones.

Humerus (*h.*).—Knight describes the humerus of *B. marshi* briefly as follows:

---

[44] Now considered the ulna, while the succeeding element is identified as the pisiform. Dr. Williston proposes the name "epipodial supernumerary" for the latter.

"Humerus about one third the length of the limb, with a stout twisted shaft that is greatly compressed near the distal end. Planes passed through the articulate ends of the humerus stand at an angle of 50°. The head is slightly rounded and is almost identical with *Ichthyosaurus*. There are three distal facets; but they are not of equal size. The facet for the ulna (see fig. 24, *u*) is the largest, the one for the radius (*r*) next in size and the one opposite the pisiform (*p*) is rudimentary, for that bone was held in cartilage and did not articulate with the humerus. The facets are elliptical in form, and those opposite the ulna and radius elongated in the plane of articulation."

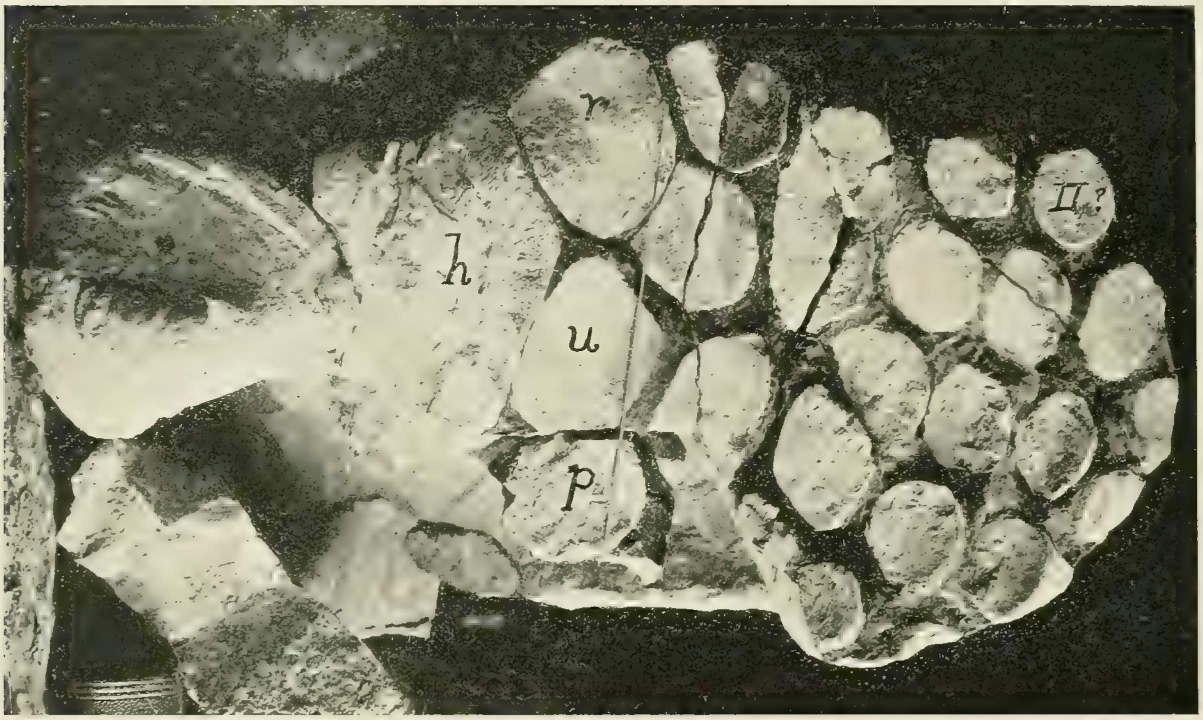


Fig. 23. Superior view of fore paddle of *Baptanodon marshi*, Knight. Reduced about 2½ times. *h*, humerus; *p*, pisiform; *r*, radius; *u*, ulna; II (?) second digit, first one wanting.

Measurements of Humeri Pertaining to English and American Forms.

	Greatest Length.	Width Proximal End.	Width Distal End.	Remarks.
No. 1955. Specimen in Yale Museum, *B. discus*......	—	100 mm.	115 mm.	Type of species.
No. 878. " " Carnegie Museum, *B. discus*...	—	115 mm.	—	Distal end wanting.
No. "S." " " Univ. of Wyoming, *B. marshi*.	190	127	130	Type of the species.
No. R. 1307. " " British Museum, *O. icenicus*...	145	—	124	
No. 47885. " " " " "	160	—	145	
Cotype *O. icenicus* in Leeds collection.....	164	115	152	Measurements given by Seeley.

Posterior Limbs. — Professor Marsh in his original description of *B. discus* describes and figures a beautifully preserved hind (?) paddle (see fig. 25) of that species. Having made a personal examination of the extremity mentioned above I find the figure to be a faithful reproduction of the limb, which clearly shows the upper limb bone as having three facets, distally as originally described. However Dr. Knight has observed that the distal extremities of the femora examined by him all have two facets only. This is important and raises the question as to the correct determination of the paddle designated as the left pelvic limb of *B. discus* by Marsh.

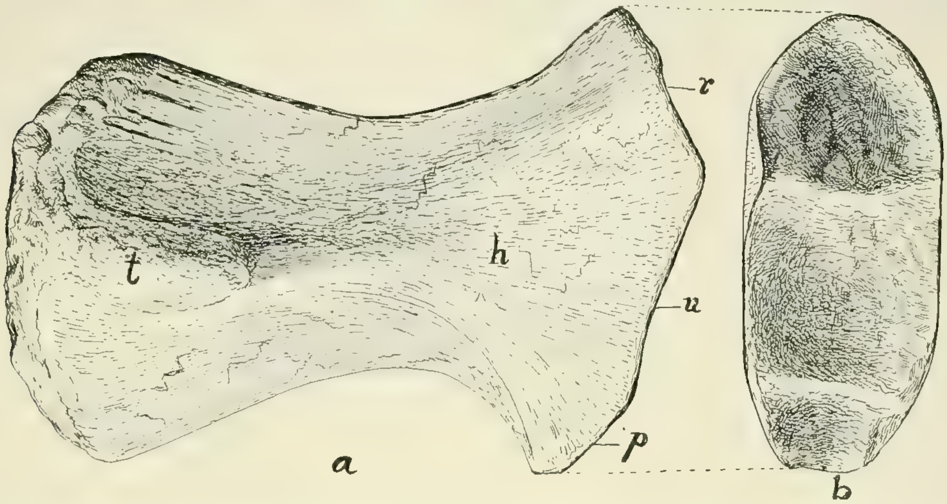


FIG. 24. (*a*) dorsal view of humerus of *Baptanodon marshi* from type specimen. One half natural size. *h*, humerus; *p*, articular surface opposite the pisiform; *r*, articular surface for radius; *t*, trochanter; *u*, articular surface for ulna. (*b*) View of distal articular end of the same. One half natural size.

This would be an important character for distinguishing the genus *Baptanodon* from the closely allied genus *Ophthalmosaurus,* which is accredited with three facets on the distal end of the femur. A photograph before me of a skeleton of *Ophthalmosaurus* shows the pelvic limb as being much smaller than the pectoral and this would strengthen somewhat the idea that Professor Marsh was mistaken in his interpretation of this extremity.

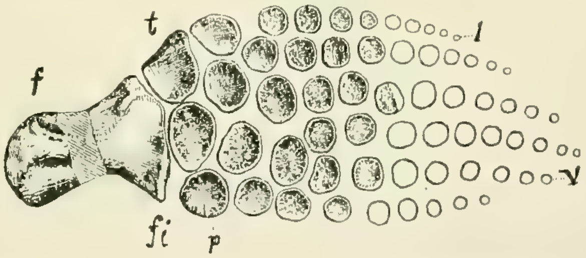


FIG. 25. Left hind (?) paddle of *Baptanodon discus* (No. 1955) seen from below. One eighth natural size. *f*, femur; *t*, tibia; *fi*, fibula; *p*, pisiform or epipodial supernumerary; *l*, first digit; *v*, fifth digit.

So far as I am able to learn there has not been a hind limb of *Baptanodon* found intact and at this time it will be impossible to definitely determine the correct solution of this problem, although from Knight's evidence and the close resemblance of this paddle to the fore limbs known, I am inclined to believe that Marsh was wrong and that the limb figured and described by him as pelvic is really a pectoral extremity. It will be noticed by an examination of Marsh's drawing (see fig. 25) that there is no contact between the proximal and distal portions of the femur (?) which renders it somewhat more difficult to make accurate comparisons.

The additional finger developed in *Baptanodon* and the fact that some of the Ichthyosaurs have as many as ten, is explained by Dr. S. W. Williston as follows :[45] "The additional fingers of the Ichthyosaurs may be also explained in a similar way. The margin of the flipper has become hardened by fibro-cartilage, which by the movement of the fingers was broken into segments, each of which finally took on ossification. A division of the phalanges by segmentation would certainly have to take place immediately in order to preserve the integrity of the paddle as an organ of propulsion. If this explanation be correct, then the additional ossification in the fore arm in the present form, as well as in the carpus, are *not* displaced elements but new ones without homologies."

Discussion of the Genus Baptanodon.

In the year 1879 Professor O. C. Marsh proposed and established the genus *Sauranodon*[46] which being preoccupied was later replaced by the name *Baptanodon*.[47] Since that time all Ichthyosaurian remains from the American Jurassic have been referred to that genus. In his original description Marsh distinguishes *Sauranodon natans* (the type species of the genus) from *Ichthyosaurus* by the absence of teeth, of which he says: "The jaws appear entirely edentulous and destitute even of a dentary groove." This statement is corroborated in a second paper[48] in the following lines: "Since the first species of the present genus was described by the writer, eight other specimens of the same group have been discovered and are now in the Yale Museum. In three of these the skull is preserved, but there are still no indications of teeth, so that we may consider these reptiles as entirely edentulous."

While cleaning the skull pertaining to specimen No. 603 preparatory to study the discovery was made that the animal had teeth,[49] two of which were found between the jaws near the end of the snout. Subsequent to this first discovery the jaws were partially separated from one another and seven more teeth were found scattered at intervals along and between the mandibles. Though no teeth were found in the dental grooves of the second specimen No. 878 rudimentary alveolar partitions (see Pl. VIII.) were present near the front together with a few faint sockets at the back of the rostrum.

---

[45] Williston, S. W., "North Amer. Plesiosaurs," Part I., *Field Columbian Museum, Pub. 73*, Geol. Series, Vol. II., No. 1, 1903, p. 70.

[46] Marsh, O. C., "A New Order of Extinct Reptiles (Sauranodonta) from the Jurassic Formation of the Rocky Mountains," *Am. Jour. of Sci.* (3), Vol. XVII.

[47] Marsh, O. C., "Note on Sauranodon," *Amer. Jour. of Sci.* (3), Vol. XIX., 1880.

[48] Marsh, O. C., "Limbs of Sauranodon, with Notice of a New Species," *Amer. Jour. of Sci.* (3), Vol. XIX. Feb., 1880.

[49] Gilmore, C. W., "Discovery of Teeth in Baptanodon, an Ichthyosaurian from the Jurassic of Wyoming," *Science*, N. S., Vol. XVI., Dec. 5, 1902.

The finding of teeth in one specimen (No. 603) and evidence of their existence at one time in a second individual (No. 878) led me to believe that dental grooves, if not teeth, would be found in the type of the genus *Baptanodon* if that specimen were thoroughly prepared. Only a little preparation was necessary to demonstrate the existence of well-developed dental grooves on both upper and lower jaws in both types, and just outside of the dental grooves imbedded in the matrix surrounding the rostrum of No. 1952[50] (*B. natans*, type of the genus) a small tooth[51] was found.

The finding of dental grooves and teeth in the types as well as their existence in two individuals preserved in the collections of this museum clearly demonstrates the fact that American Ichthyopterygians of the Jurassic possessed teeth and *were not edentulous* as originally described by Professor Marsh. Thus the one important generic character which has for so long a time separated the American form from *Ichthyosaurus*, and the closely allied European genus *Ophthalmosaurus*, has been shown to be an erroneous determination.

Among the other distinguishing characters ascribed to the type *B.* (*Sauranodon*) *natans* by Marsh, are the number and position of the sclerotic plates of the eye. He says: "The sclerotic ring is composed of eight plates. . . . These plates are not arranged in a nearly flat ring, as in *Ichthyosaurus* but form the basal segment of an elongated cone, as in the eyes of some birds." The badly crushed condition of the skull of No. 1952 makes it impossible for any one to determine with any degree of accuracy the precise number of plates composing the sclerotic circle. The right orbit, which is the better preserved, contains only two plates with the impressions of three others, the intervening space in the ring between the plates and impressions being filled with matrix. The "cone-like" position of these plates is unmistakably produced by crushing. The right orbit of No. 603 shows the sclerotic ring as having been subjected to pressure antero-posteriorly, and here we find the plates assuming the cone-like arrangement, though it is not so exaggerated as in the former case.

---

[50] Catalogue number of the Yale Museum.

[51] Gilmore, C. W., "Discovery of Dental Grooves and Teeth in the Type of Baptanodon (Sauranodon) Marsh," *Science*, N. S., XVII., No. 436, May 8, 1903, p. 750.

[52] Type of the species, *B. discus*.

The left orbit of the same specimen has the ring nearly circular (see Pl. X., fig. 2) and the plates quite flat, though as Frass has pointed out in life they were probably arranged at somewhat more of an angle. It might be well to mention here that the sclerotic ring in the skull of 1955 [52] (*B. discus*) shows the same flat circular arrangement of the plates observed among most of the members of the *Ichthyosauria.*

The specific characters given by Marsh for separating the two species of *Baptanodon* are quite as superficial as the generic characters just reviewed. Size alone is the only difference of importance, but as in most reptiles these probably continued to grow throughout life. "The breadth of paddles," "elongation of the facial portion of the skull," "slender snout," etc., are illusionary characters and would not serve to distinguish the two species. For example in giving the distinguishing characters between *B. discus* and *B. natans* (type of the genus) Marsh says: "The paddles, also are broader in proportion to their size, than in the type species." It is now definitely understood that the extremities of *B. natans* are unknown. However in the Catalogue of Fossil Reptilia and Amphibia in the British Museum, fig. 5, p. 7, is a figure of the left pelvic limb of *B. natans* (after Marsh from the *Proc. Geol. Society*).[53] The illustration shows the dorsal surface of the limb and is to all intents the reverse view of the left pelvic (?) limb of *B. discus* and accidentally referred to the wrong species.

In a more recent paper[54] the late Dr. W. C. Knight has added much to our knowledge of *Baptanodon* besides giving reasons for considering this genus distinct from *Ophthalmosaurus.*

To correct some inaccuracies in the characters enumerated I will take up the arguments advanced by him and make such comments as access to literature and more complete and better preserved material render possible.

They are as follows:

"In comparing the limbs of *Ophthalmosaurus* and *Baptanodon* one should consider the following points:

1. In *Baptanodon* the humerus is about one third the length of the limb."

1. The absolute length of limb in either form apparently unknown, but in so far as one may judge from illustrations the limbs of the two forms appear to have about the same proportions. Lydekker in the catalogue of Fossil Reptilia and Amphibia in the British Museum gives measurements of

---

[53] Nicholoson and Lydekker have the same illustration in their "Manual of Paleontology," Vol. II., Fig. 1034, and ascribed to the same species, though (after Marsh and Hulke).

[54] Knight, W. C., "Some Notes on the Genus Baptanodon with a Description of a New Species," *Amer. Jour. Sci.* (4) Vol. XV.

	the humerus of *O. icenicus* which agree essentially with the measurements of the American forms.
2. "It has a twisted shaft which is greatly compressed."	2. A humerus pertaining to a specmen of *O. icenicus* preserved in the collections of the American Museum of Natural History, shows the same characters.
3. The distal facets are all unequal in size and one of them is merely rudimentary, besides they are elliptical in the plane of articulation."	3. The humerus of *O. icenicus* has three unequal facets on the distal end, though the one for the pisiform could hardly be considered as rudimentary. The facets on the distal end of the humerus mentioned above are elliptical in the plane of articulation. Dr. Knight must have drawn his conclusions from a comparison of the humerus of *B. marshi*, with the humerus of *O. cantabrigiensis* a second species described by Lydekker, which has three subequal facets, the longer axis being vertical to the plane of articulation. The former species (*O. icenicus*) however is the type of the genus.
4. "There is also an abnormal number of digits and the arm is much more powerful and larger than found in *Ophthalmosaurus* of equal size."	4. So far as known *Ophthalmosaurus* only has five digits and as Knight has observed the limb of *Baptanodon* was probably more powerful to the extent of being broader, though the other proportions appear remarkably similar
5. "In comparing *Baptanodon* with *Ophthalmosaurus* it will be well to consider that in *Baptanodon* the interclavicle is either rudimentary or wanting."	5. It is now positively known that *Baptanodon* has a well-developed interclavicle. See description, this paper, p. 36.
6. "The absence of the intercentra between the second and third vertebræ."	6. The absence of this bone in other species of *Baptanodon* besides *B. marshi* has yet to be demonstrated, for

	it has already been shown that two specimens in this museum, Nos. 603 and 878, have a surface on the infero-posterior margin of the axis as if for the articulation of such a bone. However this element has never been found in place.
7. "The development of large facets upon the interior margins of the coracoids."	7. The coracoids of *O. icenicus* examined by me at the American Museum of Natural History, New York, N. Y., show well-developed surfaces for articulation with one another medially.

Combining the characters given by Marsh and Knight with those shown by the material under discussion the genus *Baptanodon* may now be distinguished by the following characters:

Gen. char.: *Teeth present but loosely attached. Dentition somewhat reduced but extending the entire length of the jaws. Opisthotic reaching and partially enclosed by the squamosal. Reduced number of hypocentra. Vertebral centra forward of the posterior caudals uniformly biconcave. Ribs of the anterior part of the skeleton double-headed. Clavicles firmly united. Well developed interclavicle present. Coracoids without posterior notch and uniting in the median line by large elliptical facets. Humerus with strongly developed trochanteric ridge on dorsal surface and having three unequal facets on the distal extremity, which articulate with three irregular polygonal elements in the epipodial row. All remaining bones of the anterior extremities more or less rounded and retained in persistent cartilage.*

Three species of this genus have been described, of which a brief review is given in the following pages.

BAPTANODON NATANS, Marsh.

Sauranodon natans, Marsh, O. C., Amer. Jour. of Sci., Vol. XVII., 1879.
Baptanodon natans, Marsh, O. C., Amer. Jour. of Sci., Vol. XIX., 1880.
Ophthalmosaurus natans, Lydekker, R., Geol. Mag., Vol. V., 1888.
Baptanodon natans, Lydekker, R., Cat. of Fossil Reptilia and Amphibia in the British Museum, Part II., 1889.

This species, the type of the genus, was based upon a considerable portion of a skull, a number of vertebræ and ribs, and parts of one or more limb bones. As has been shown previously hardly any of the original characters given for this species can be considered valid.

B. natans is typically the smallest species of this group. In fact until the type specimen is properly prepared and redescribed this is the only way by which *B. discus* may be distinguished from this form. The teeth when better known may show specific differences. The one tooth discovered of *B. natans* has a smooth enameled surface as contrasted with striated surfaces of the teeth of *B. discus.*

The type No. 1952 was collected by Mr. W. H. Reed, in the vicinity of Como Bluff, Albany Co., Wyoming, and is now preserved in the collections of the Yale Museum, New Haven, Conn.

BAPTANODON DISCUS, Marsh.

Sauranodon discus, Marsh, O. C., Am. Jour. of Sci., Vol. XIX., 1880.
Baptanodon discus, Marsh, O. C., Am. Jour. of Sci., Vol. XIX., 1880.
Ophthalmosaurus discus, Lydekker, R., Geol. Mag., Vol. V., 1888.
Baptanodon discus, Lydekker, R., Cat. of Fossil Reptilia and Amphibia in the British Museum, Part II., 1889.
Microdontosaurus petersonii, Gilmore, C. W., Science, N. S., Vol. XVI., 1902.

This species was based upon a portion of a poorly preserved skull, numerous vertebræ including the coalesced atlas and axis, left coracoid, with the greater portion of the left pelvic (?) paddle and numerous fragments of other portions of the skeleton.

It is with considerable trepidation that I assign the specimens considered in this paper to the species *discus,* but after a somewhat superficial examination of the type I was unable to find differences of sufficient importance to warrant the establishment of a new species as was proposed in a previous paper. The study of the type was superficial to the extent of trying to determine characters from material that has been but little prepared. The parts of the skull exposed only show a small area of the mid-portion of the rostrum and one sclerotic ring; the other parts are either wanting or covered by the very refractory matrix. The characters shown by the parts of the skull exposed together with the atlas and axis and left coracoid are the principal elements upon which my comparisons were based. The great similarity of these elements to the corresponding parts of our specimens prompted me to the present determination.

The type specimen No. 1955 is preserved in the vertebrate collections of the Yale Museum, New Haven, Conn. It was collected by Mr. W. H. Reed in Wyoming.

BAPTANODON MARSHI, Knight.

Baptanodon marshi, Knight, W. C., Amer. Jour. of Sci. (4), Vol. XV., 1903.

In the characterization of this species Dr. Knight distinguished it from all others by the shape and arrangement of the bones of the fore paddle. The two important differences which he considered as typical are the consolidation of three elements into one in the third segment and the development of the abnormal number of digits by a division of the third finger. Accompanying the description is a drawing of the right pectoral limb showing the paddle as retained in the matrix. A photograph of the same paddle is shown in fig. 23.

The paddle probably had six digits but the greatest transverse segmentation of the parts preserved only shows five elements, although in the original description he says: "The limb that I have been studying and figured differs from the one published by Marsh, inasmuch as the abnormal number of digits do not appear until the phalanges are reached." As the specimen does not show an abnormal number of digits it would be assuming considerable, because of the peculiar arrangement of the bones of the paddle in this form, to say definitely at what point the extra digit, if it did exist, is developed. Moreover it does not appear justifiable to compare this fore limb with the supposed hind paddle of *B. discus* and consider as specific characters differences that are almost certain to exist in the structure of anterior and posterior paddles.

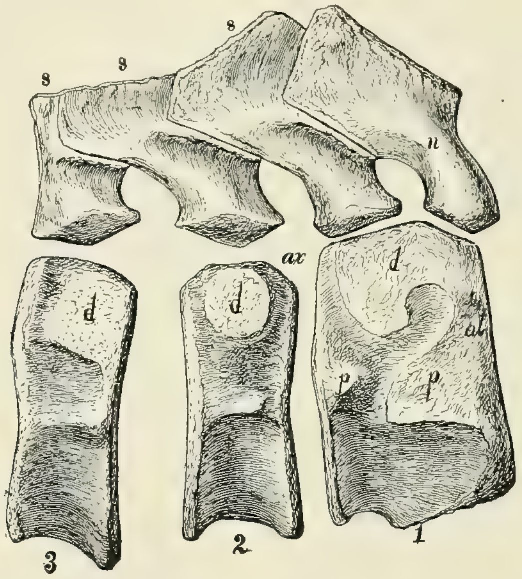


FIG. 26. Atlas, axis and third and fourth cervicles of *Baptanodon marshi* ("S"). Seen from the right side. Type specimen. One half natural size. 1. Coalesced atlas and axis. 2 and 3. Third and fourth cervicles. *at*, atlas; *ax*, axis; *d*, diapophysis; *p*, parapophysis; *n*, paired neural arch.

After an examination of the type I should consider the large element (see Fig. 23) as due to a consolidation of two rather than three elements. An offset on the distal border apparently indicates the point of union. This consolidation, instead of being a normal character, may be due to pathological conditions as has been shown to exist in the extremities of the *Mososaurs*.[55]

The species was based upon a considerable portion of the pectoral girdle, with a part of the right fore limb and 41 consecutive vertebræ extending from the atlas posteriorly.

A comparison of the coalesced atlas and axis of *B. marshi*, with the same elements of *B. discus* appears to show differences that would serve for specific separation, *i. e.*, the reduced number of intercentra, shown by the absence of the apophysis on the axis for the third incentrum, and the reduced size of the parapophyses of the third and fourth cervicles. These were certainly not functional in this species. Some other minor differences will be noted by comparing Figs. 10 and 26.

With these exceptions and the arrangement of the bones of the paddle the other parts preserved do not differ materially from the corresponding elements of *B. discus*.

The type is specimen "S" preserved in the Jurassic collections of vertebrates of the University of Wyoming, at Laramie, Wyoming. This specimen was collected by Mr. W. H. Reed from the Baptanodon Beds of the Jurassic in the Northern part of Albany Co., Wyoming, in 1897.

Discussion of the Genus Ophthalmosaurus.

In studying the genus *Baptanodon* it was necessary to review the literature pertaining to the closely allied genus *Ophthalmosaurus*. Having this at hand and because of the great similarity of the two forms it is believed that a brief review of that genus would be appropriate at this time.

The type species is *O. icenicus* founded by Seeley[56] on the greater portion of the pectoral girdle. The important characters by which he distinguishes this genus from *Ichthyosaurus* are the peculiar conditions found in the clavicular girdle, *i. e.*, the separated clavicles, the enclosing of the anterior part of the interclavicle in a groove of the clavicles, and the embracing of the anterior margins of the coracoids by the clavicles.

Further characters were made known by the description of a portion of the fore limb of a second individual which is larger and better preserved than the corresponding elements of the type. These differences are as follows: distal end of humerus articulating with three bones, radius, ulna and olecranon (pisiform of modern nomenclature) and the carpus with a row of four elements.

The characters cited above constitute all of the essential differences given. The somewhat remarkable supposition that the clavicles encircled the coracoids is due to Professor Seeley's incorrect determination of the borders of the coracoid, as has already been indicated by Lydekker,[57] "the one marked intercoracoidal being really the glenoid cavity." This correction is substantiated by the material under consideration in this paper, and the clavicles instead of enclosing the coracoids (made impossible by the articulation between coracoid and scapula), curved up in front of the scapulæ as in *Ichthyosaurus.*

---

[55] Williston, S. W., "Univ. Geol. Survey of Kansas," Vol. IV., Part I., p. 244.

[56] Seeley, H. G., *Quart. Jour. Geol. Society of London*, Vol. XXX.

In 1888 in the "Catalogue of Fossil Reptilia and Amphibia in the British Museum," Lydekker gave the following characterization of the genus:

"Teeth present but apparently small, and perhaps confined to the anterior portions of the jaws. Humerus and femur with strongly developed trochanteric ridge on dorsal surface, and articulating distally with three bones, as in *Baptanodon,* which are of irregular polygonal contour. The ulna being pentagonal. Clavicles (typically) separate, with the interclavicle wedged in between them. Vertebral centra of the general type of those of Campyldont subgroup of *Ichthyosaurus.* Coracoid without posterior notch. Humerus and femur apparently (except at distal end) of the general type of those of *I. campylodon* and relatively large in proportion to the vertebræ. In *Baptanodon* and probably also in this genus both pectoral and pelvic limbs relatively wide (or that arising from the intermedium) contains two such rows, with the consequent presence of two centralia."

In 1898 Woodward[58] confined most of the observations made by Seeley and Lydekker, and added important information concerning the pelvic region, *i. e.,* "The pubis and ischium are fused together, leaving a small obturator foramen." Besides, he figures a right pectoral limb which shows that member as being composed of the normal number of five digits.

Combining the characters given by the different authorities the genus *Ophthalmosaurus* may be distinguished by the following:

Gen. char.: *Teeth present but apparently small and perhaps confined to the anterior portions of the jaws. Clavicles (typically) separate with the interclavicle wedged in between them. Coracoids without posterior notch. Humerus and femur with strongly developed trochanteric ridge on dorsal surface and articulating distally with three bones, which are of irregular polygonal contour. Ulna is pentagonal. Pubis and ischium fused together, leaving a small obturator foramen.*

Two species of this genus have been described of which a brief review is given The type specimens are from the Jurassic and Lower Cretaceous of England.

---

[57] Lydekker, R., "Cat. of Fossil Reptilia and Amphibia in the British Museum." Part II.

[58] Woodward, A. S., "Vertebrate Palæontology," p. 183.

OPHTHALMOSAURUS ICENICUS, Seeley.

Ophthalmosaurus icenicus, Seeley, H. G., Quart. Jour. of the Geol. Soc. of London. Vol. XXX., 1874, pp. 696–707.

This, the type species of the genus, was based upon quite a complete pectoral girdle and portion of a fore limb, the latter pertaining to a second individual. The type was found in the Oxford clay by Mr. C. Leeds, who later submitted it to Professor Seeley for description. The remains of four or five individuals preserved in the collections of the British Museum, and referred to this species by Lydekker have all been found in the Kimmeridge clays which is considered Upper Jurassic, while the type is from Middle Jurassic.

The following specific characters constitute the essential differences as characterized by Lydekker in the Catalogue of Fossil Reptilia and Amphibia in the British Museum.

Sp. char.: "*Larger than the type of the following species. The post-axial facet smaller than that of the radius; and the antero-posterior diameter of the proximal extremity of the humerus less than that of the distal extremity. In the cervical region the cupping of the anterior face of the centrum confined to the central portion and surrounded by a flattened periphery.*

OPHTHALMOSAURUS CANTABRIGIENSIS, Lydekker.

Ophthalmosaurus cantabrigiensis, Lydekker, R., Geol. Mag., Decade III., Vol. V., July, 1888, No. 7, p. 309.

This species was first proposed by Lydekker in a note to the Geological Magazine, the description appearing later in the Catalogue of the Fossil Reptilia and Amphibia in the British Museum. The material upon which this species is based consists of a right humerus from the Cambridge Greensand.

The equal size of the three distal facets of the humerus, and their greatest elongation being vertical to the plane of articulation at once distinguishes this species from *Baptanodon*. Lydekker in his original description adds, "This species may belong to *Baptanodon*." In reality the type of the genus (*O. icenicus*) is more closely allied to that genus.

The type, No. 43989, is preserved in the British Museum.

Sp. char.: "*Typically of small size. The three distal facets of the humerus nearly equal in size, and the antero-posterior diameter of the proximal extremity of the same bone exceeding that of the distal.*"

Relationship and Classification.

In the general outlines of its structure, *Baptanodon* appears very similar to the European genus *Ophthalmosaurus*, although the true relationship of the two genera has long been an enigma to scientists.

In 1888 Lydekker[59] considered *Baptanodon* a synonym of *Ophthalmosaurus* after Baur's[60] suggestion, that: "*Ophthalmosaurus*, Seeley. Vielleicht nicht verschieden von Baptanodon," a view which he abandons later in the Catalogue of Fossil Reptilia and Amphibia in the British Museum.

In 1898 Woodward in his Vertebrate Paleontology, p. 183, observes: "*Baptanodon* from the Jurassic of Wyoming is remarkably similar to the European fossil and perhaps generically identical."

A number of equally eminent American paleontologists have verbally expressed themselves as believing the two genera synonymous.

The presence of firmly united clavicles without suture, and the uniform biconcave cupping of the anterior cervicals, together with the development of a sixth digit in *Baptanodon* are characters which appear to be of sufficient value to warrant the distinct separation of the two genera.

In the reduced size and loose attachment of the teeth, the arrangement of the bones of the anterior extremities, and the retention of the disk-like elements of the paddles in persistent cartilage, these two forms are very similar.

The characters enumerated above indicate a high degree of aquatic specialization and *Baptanodon*, I believe, should be considered the most specialized of the known *Ichthyopterygia*. The closest affinities of *Baptanodon* are with *Ophthalmosaurus*, next approached by *Ichthyosaurus*. In some respects *Baptanodon* is but little more modified to purely aquatic conditions than is found in the earlier genus *Shastasaurus* from the Triassic of California. The humerus of *Baptanodon* is not so broad as that of *Shastasaurus* but it shows greater specialization in the development of three unequal facets on the distal end.

The reduction in the number of intercentra in *Baptanodon marshi*, as well as in *Baptanodon discus*, appears to indicate the most specialized character of the genus. The separated zygapophysial facets in the cervical region, which become single in the vertebræ more posteriorly, are approximated in the Ichthyosaurs.

If Baur's classification of the *Ichthyopterygia* be accepted the family Baptanodontidæ proposed by Marsh would include the two genera *Baptanodon* and *Ophthalmo-*

---

[59] Lydekker, R., *Geol. Mag.*, Vol. II., p. 309.

[60] Baur, G., "Ueber den Ursprung der Extremitäten der Ichthyopterygia," *Bericht der XX. Versammlung der Oberrhein. geol. Ver.*, Vol. XX.

saurus. The family would be distinguished by the peculiar arrangement of the bones of the paddles, and the reduction of the number of intercentra.

The classification of the genus *Baptanodon* would then be best expressed by the following:

Class, Reptilia; Order, Ichthyosauria; Family, Baptanodontidæ; Genus, Baptanodon.

Bibliography.

Baur, G. On the Morphology and Origin of the Ichthyopterygia, *Amer. Naturalists*, Vol. XXI., 1887, pp. 837–840; Ueber den Ursprung der Extremitäten der Ichthyopterygia, *Bericht der XX. Versammlung des Oberrhein geol. Ver.*, Vol. XX., 1887.

Bauer, F. Osteologische Notizen über Ichthyosaurier, *Anat. Anzeiger*, Vol. XVIII., 1883, pp. 574–588.

Cope, E. D. On the Homologies of Some of the Cranial Bones of the Reptilia and on the Systematic Arrangement of the Class, *Proc. Amer. Assoc. Adv. of Sci.*, Vol. XIX., 1870, pp. 194–247; A New Genus of Ichthyoptergyia, *Amer-Naturalist*, Vol. XIII., 1879, p. 271.

Frass, F. Die Ichthyosaurier der Süddeutschen Trias und Jura Ablagerungen. Tübingen, 1891.

Gilmore, C. W. Discovery of Teeth in Baptanodon, an Ichthyosaurian from the Jurassic of Wyoming, *Science*, N. S., Vol. XVI., 1902, No. 414, pp. 913–915; Discovery of Dental Grooves and Teeth in the Type of Baptanodon (Sauranodon) Marsh, *Science*, N. S., Vol. XVII., 1903, No. 436, p. 750.

Hatcher, J. B. Osteology of Haplocanthosaurus, *Memoirs Carnegie Museum*, Vol. II., 1903, No. 1, p. 70–71.

Hulke, J. W. Anniversary Address of the President Geol. Soc. of London, *Quart. Jour.*, Vol. XXXIX., 1883, pp. 44–64.

Knight, W. C. Jurassic Rocks of Southeastern Wyoming, *Bulletin of the Geol. Soc. of Am.*, Vol. II., 1900, pp. 377–388; Some Notes on the Genus Baptanodon, with a Description of a New Species. *Am. Jour. of Science* (4), Vol. XV., 1903.

Loomis, F. B. On Jurassic Stratigraphy in Southeastern Wyoming, *Bull. of the Am. Museum of Nat. History*, Vol. XIV., article XII., 1901, pp. 189–197.

Lydekker, R. Note on the Classification of the Ichthyopterygia (with a notice of two new species), *Geol. Mag.*, Decade III., Vol. V., No. 7, 1888, p. 309–314; Catalogue of the Fossil Reptilia and Amphibia in the British Museum, 1889.

Marsh, O. C. A New Order of Extinct Reptiles (Sauranodonta) from the Jurassic Formation of the Rocky Mountains, *Amer. Jour. of Sci.* (3), Vol. XVII., 1879, pp. 85–86; The Limbs of Sauranodon with Notice of a New Species, *Amer.*

Jour. of Sci. (3), Vol. XIX., 1880, pp. 169–171; Note on Sauranodon, *Amer. Jour. of Sci.* (3), Vol. XIX., 1880, p. 491; The Reptilia of the Baptanodon Beds, *Am. Jour. of Sci.* (3), Vol. L., 1895, pp. 405–406; Vertebrate Fossils of the Denver Basin, Monograph U. S. G. S., Vol. XXVII., 1897.

Merriam, J. C. Triassic Ichthyopterygia from California and Nevada. *Univ. of Cal. Publications,* Vol. III., 1902, No. 4, pp. 63–198; New Ichthyosauria from Upper Triassic of California, *Univ. of. Cal. Publications,* Vol. III., 1903, No. 12, pp. 249–263.

Nicholoson and Lydekker. Manual of Paleontology, Vol. II., 1889.

Owen, R., Monograph of the Fossil Reptilia of the Liassic Formations. *Owen's British Fossil Reptiles,* Vol. VII., 1881, part third, pp. 83–134.

Seeley, H. G. On the Pectoral Arch and Fore-Limb of Ophthalmosaurus, a new Ichthyosaurian genus from the Oxford Clay (read June 24, 1874). *Quart. Jour. of the Geol. Soc. of London,* Vol. XXX., 1874, pp. 696–707.

Williston, S. W. North American Plesiosaurs. *Field Columbian Museum Publications.* No. 73, Geol. Series, Part I., Vol. II., No. 1, 1903.

Explanation of Plates.

Plate VII. Diagram showing the position of the elements of specimen No. 878, *Baptanodon discus,* as they lay imbedded in the concretion. The irregular line surrounding the bones represents the outline of the concretion. *at.,* atlas; *co.,* coracoid; *cl.,* clavicle; *h.,* humerus; *i.cl.,* interclavicle; *n.,* paired neural arch of atlas; *o.occ.,* occipital condyle; *r.,* ribs; *s.,* spinous process of the vertebræ; *sc.,* scapula.

Plate VIII. Side view of skull of *Baptanodon discus,* Marsh (No. 878). One fifth natural size. Restored. *ag.,* angular; *d.,* dentary; *j.,* jugal; *la.,* lachrymal; *mx.,* maxillary; *na.,* nasal; *nar.,* narial opening; *occ.c.,* occipital condyle; *pa.,* parietal; *pmx.,* premaxillary; *prf.,* prefrontal (?); *ptf.,* postfrontal; *pto.,* postorbital; *q.j.,* quadrato-jugal; *q.u.,* quadrate; *s.ag.,* surangular; *s.t.,* supratemporal; *scl.,* sclerotic plates; *sta.,* stapes; *spl.,* splenial; *sq.,* squamosal.

Plate IX. 1. Top view of same skull. One fifth natural size. Restored. *art.,* articular; *ex.occ.,* exoccipital; *fr.,* frontal; *na.,* nasal; *nar.,* nares; *occ.c.,* occipital condyle; *pa.,* parietal; *pin.,* pineal foramen; *pmx.,* premaxilla; *prf.,* prefrontal (?); *ptf.,* postfrontal; *s.ag.,* surangular; *s.occ.,* suraoccipital; *s.t.,* supratemporal; *s.t.f.,* supratemporal fossa; *sq.,* squamosal.

2. Inferior view of skull of *Baptanodon discus* (No. 603). One fifth natural size. Restored. *ag.,* angular; *b.occ.,* basioccipital; *b.s.,* basisphenoid; *d.,* dentary; *ipt.,* interpterygoid vacuity; *occ.c.,* occipital condyle; *pl.,* palatine; *prs.,* presphenoid; *pt.,* pterygoid; *spl.,* splenial; *v.,* vomer. The suture between *ag.* and *spl.* and *cor.,* is incorrectly placed posteriorly.

Plate X. 1. Side view of skull of *Baptanodon discus,* Marsh (No. 878). One fifth natural size. Seen from right side.

2. Side view of skull of *Baptanodon discus,* Marsh (No. 603). One fifth natural size. Seen from left side.

Plate XI. 1. Posterior view of skull of *Baptanodon discus* (No. 878). *th.,* thyrohyal.

2. The same, restored. One fifth natural size. *ag.,* angular; *art.,* articular; *b.occ.,* basioccipital; *b.s.,* basisphenoid; *cor.* (?), coranoid; *ex.occ.,* exoccipital; *f.m.,* foramen magnum; *occ.c.,* occipital condyle; *op.o.,* opisthotic; *pa.,* parietal; *pt.,* pterygoid; *q.j.,* quadrato-jugal; *qu.,* quadrate; *s.ag.,* surangular; *s.occ.,* supraoccipital; *s.t.,* supratemporal; *sta.,* stapes; *s.t.f.,* supratemporal fossa; *sq.,* squamosal.

Plate XII. 1. Anterior view of pectoral girdle of *Baptanodon* (No. 919). One fifth natural size. *co.,* coracoids; *sc.,* scapulæ; *x.,* surfaces for clavicles.

2. Dorsal view of the same girdle. One fifth natural size. Lettering same as 1.

3. Ventral view of pectoral girdle *Baptanodon discus* (No. 878). One fifth natural size. Restored. *cl.,* clavicle; *i.cl.,* interclavicle; *h.,* humerus. Other lettering same as figures 1 and 2.

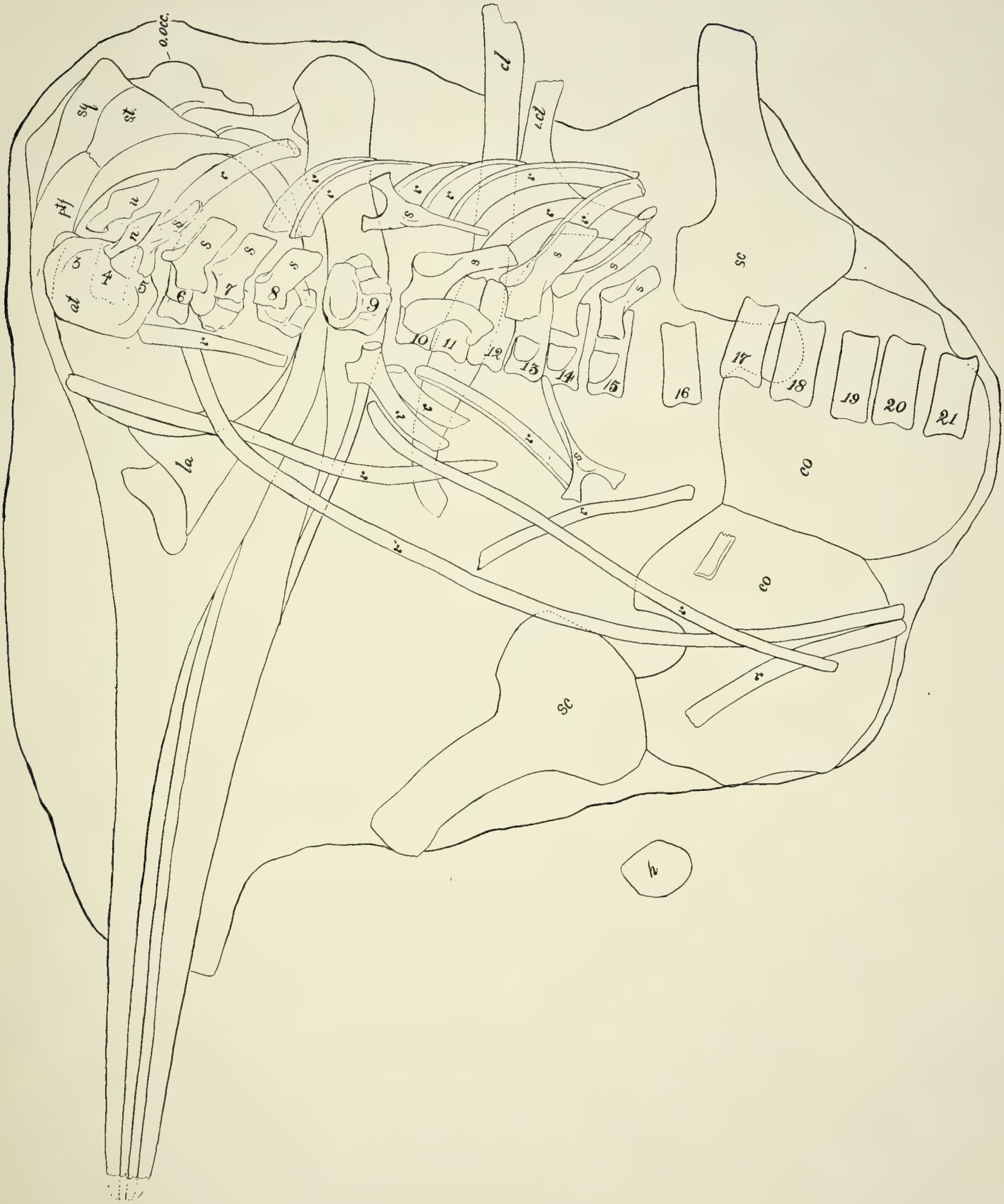
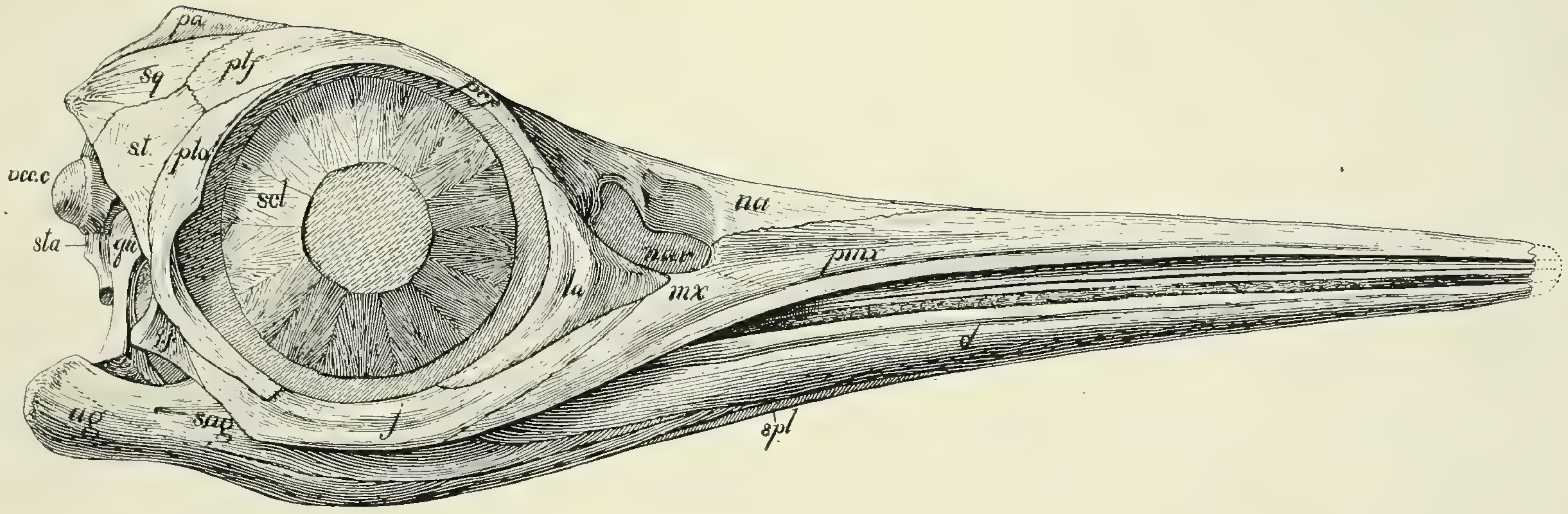
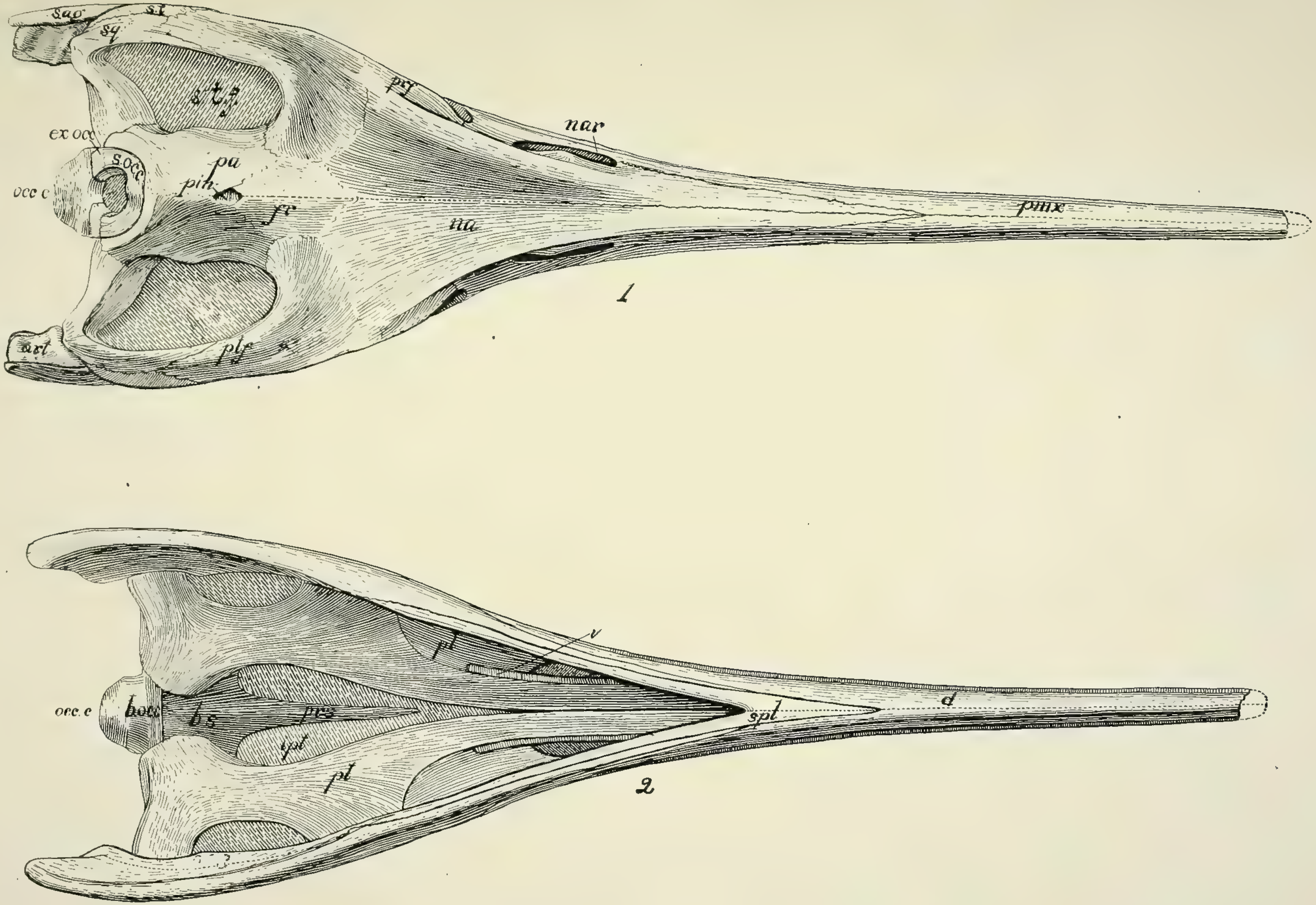


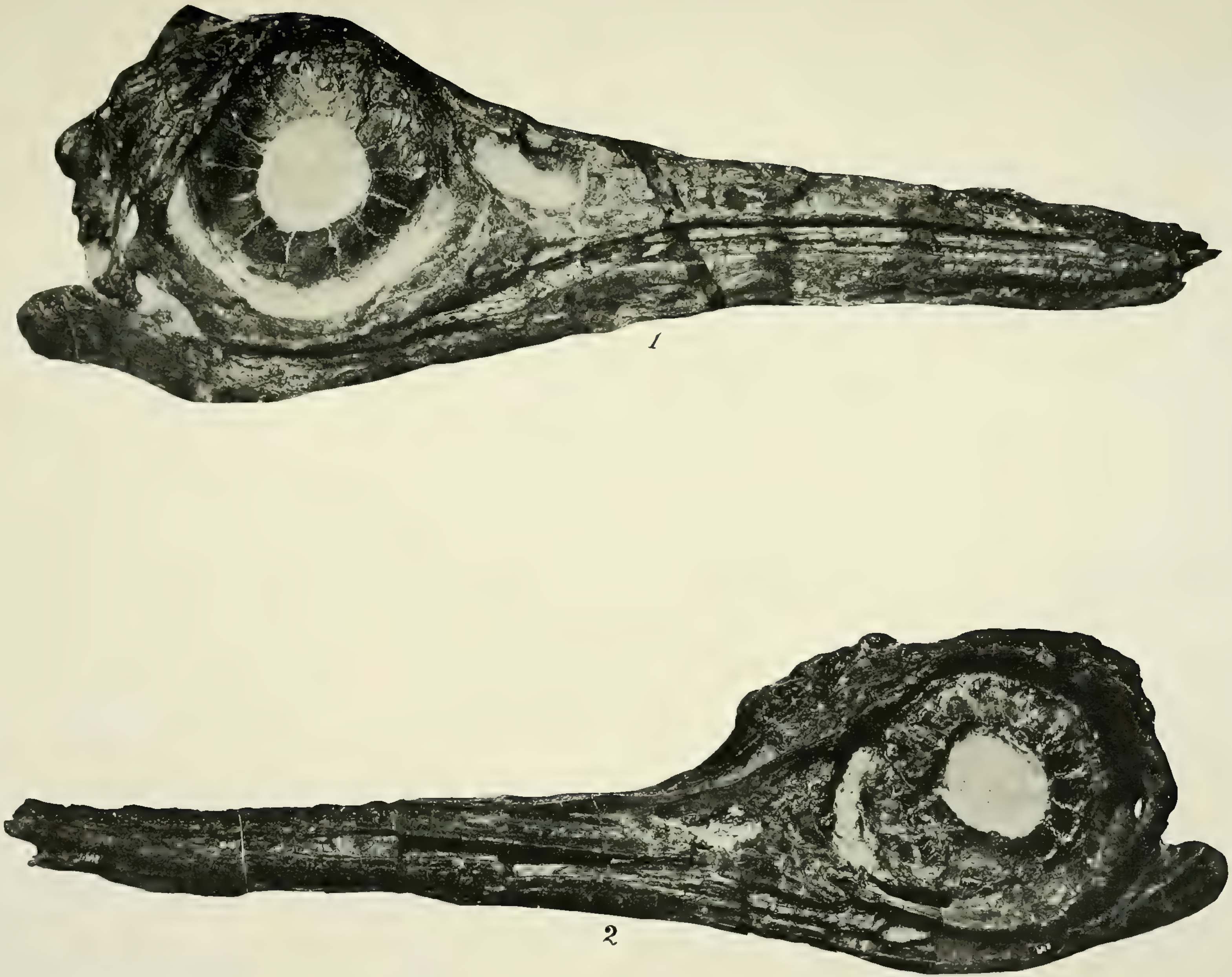
DIAGRAM SHOWING THE POSITION IN WHICH THE ELEMENTS OF THE SPECIMEN OF *BAPTANODON DISCUS* MARSH (No. 878) WERE FOUND IMBEDDED IN THE CONCRETION. $\frac{1}{5}$ NATURAL SIZE.



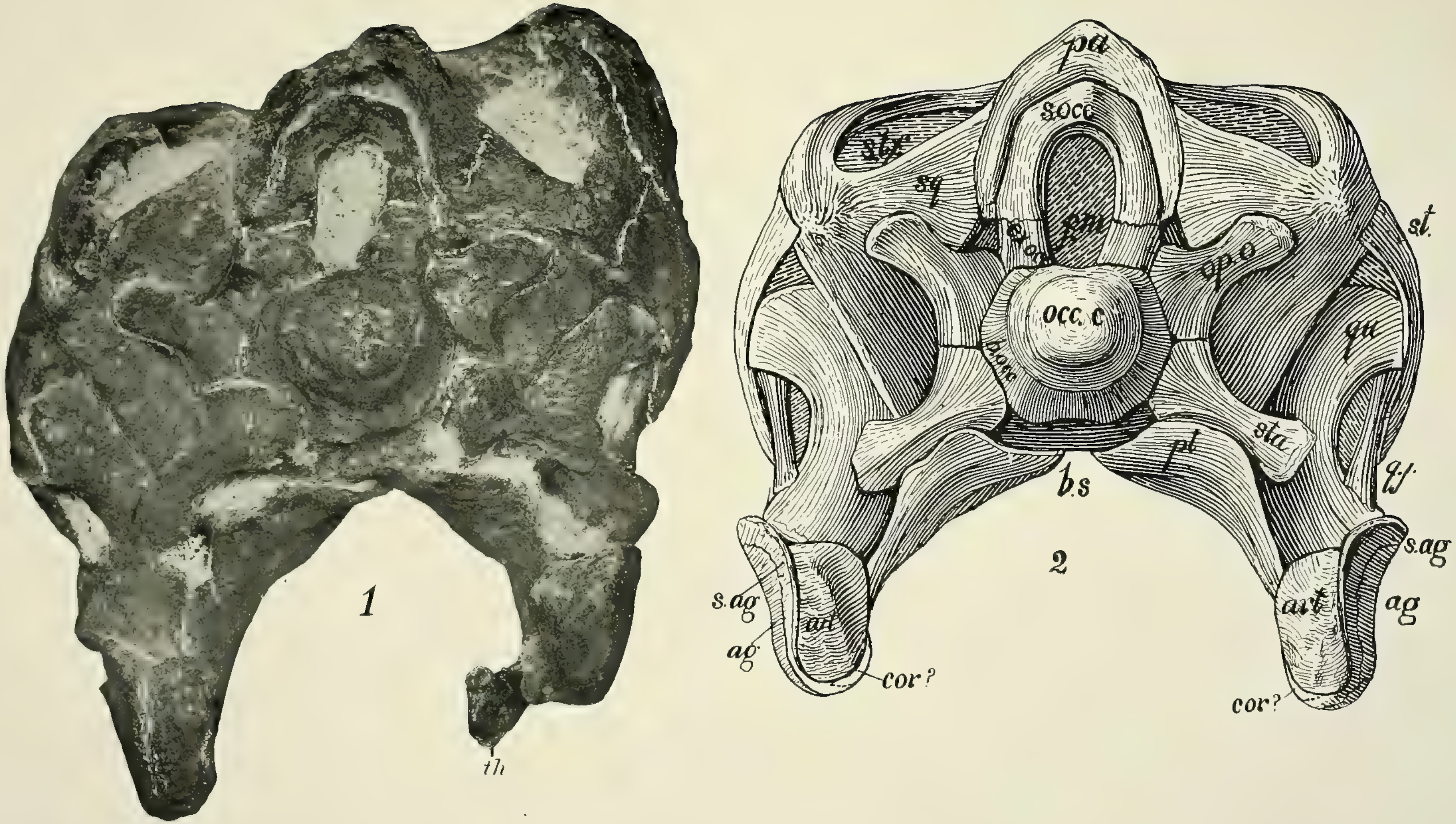
SIDE VIEW OF SKULL OF *BAPTANODON DISCUS* MARSH (No. 878). $\frac{1}{5}$ NATURAL SIZE. RESTORED.



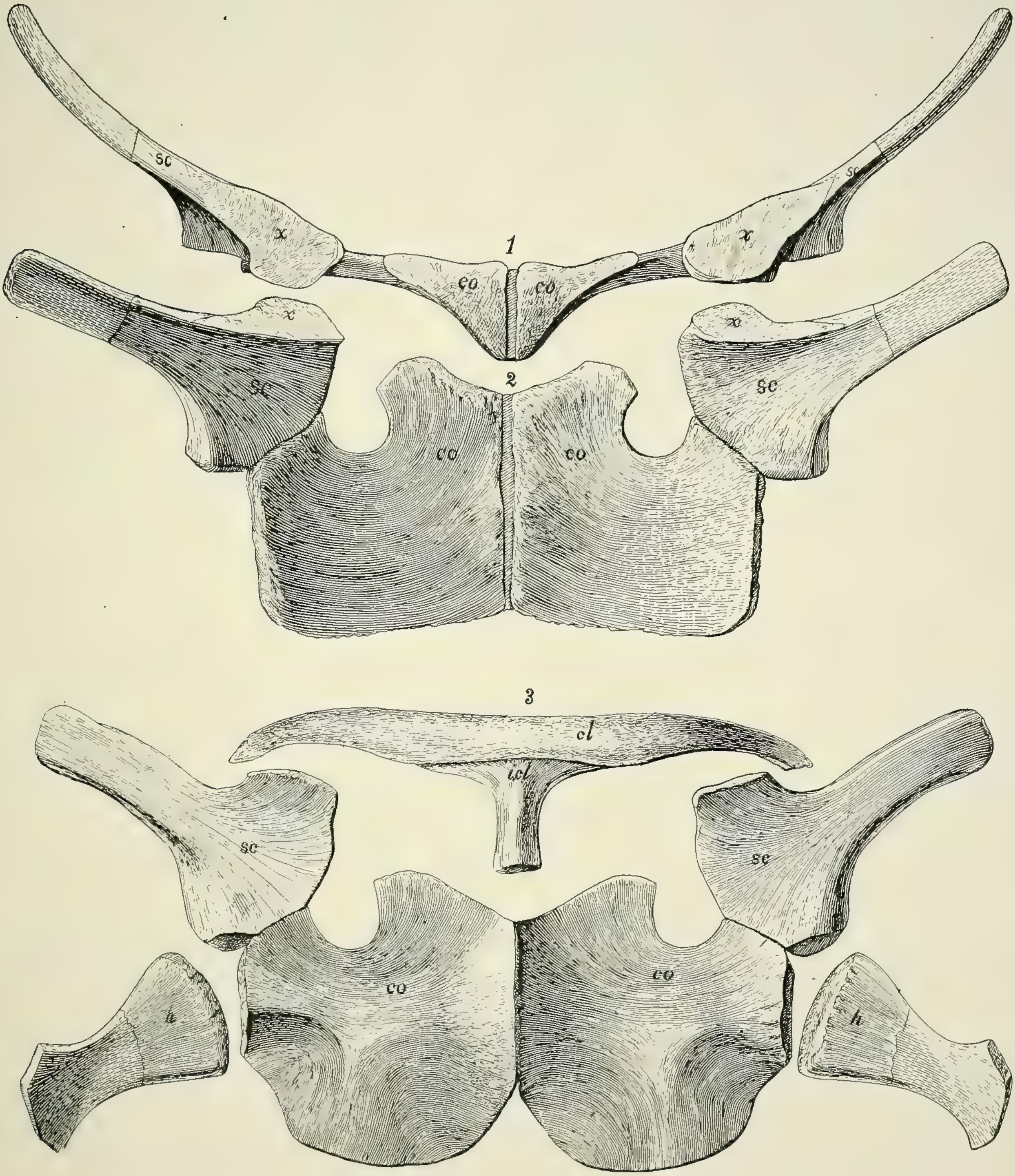
SKULL OF *BAPTANODON DISCUS*. 1, SUPERIOR VIEW (NO. 878); 2, INFERIOR VIEW (NO. 603). BOTH $\frac{1}{5}$ NATURAL SIZE.



SKULLS OF *BAPTANODON DISCUS.* 1, SIDE VIEW (No. 878) $\frac{1}{5}$ NATURAL SIZE; 2, SIDE VIEW (No. 603) $\frac{1}{5}$ NATURAL SIZE.



POSTERIOR VIEWS OF THE SKULL OF *BAPTANODON DISCUS.* (No. 878) $\frac{1}{5}$ NATURAL SIZE. 1, SPECIMEN AS FOUND; 2, RESTORED.



PECTORAL GIRDLE OF *BAPTANODON DISCUS.* 1, ANTERIOR VIEW; 2, DORSAL VIEW (No. 919); 3, VENTRAL VIEW (No. 878). ALL $\frac{1}{5}$ NATURAL SIZE.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 3.

FOSSIL AVIAN REMAINS FROM ARMISSAN.

By C. R. Eastman.

The history of gallinaceous birds is traceable as far back as the Middle Eocene, the earliest known genus being found in the Green River limestone of Wyoming. This is known by a single, nearly perfect skeleton, and seems to be closely related to the existing *Ortalis*. From the Upper Eocene of the Paris Basin have been described two species of *Palæortyx*, which comprise small pheasant-like birds, with the rostrum longer and less curved than in modern forms. Certain fragments occurring in the Quercy Phosphorites (Upper Eocene), and the calcareous marl of Vaucluse, supposed to be of equivalent age, are likewise referred to *Palæortyx*, and several species are also known from the Miocene of Southern France. The remarkable and highly specialized Hoactzin, or *Opisthocomus*, of South America, whose habits and certain points of structure suggest considerable affinity with the *Cuculi*, is represented by a closely similar genus (*Filholornis*) in the Phosphorites of Quercy.

The fresh-water limestone of Armissan, near Narbonne (Aude), by some geologists regarded as of Upper Eocene, by others as of Oligocene age, has furnished remains of a single genus (*Taoperdix*), which agrees somewhat closely with modern pheasants; and *Phasianus* itself occurs rather abundantly in the Middle and Upper Miocene, and also in the Lower Pliocene of Pikermi, where it is accompanied by *Gallus*. A species of fossil turkey (*Meleagris antiquus*) is known from the White River Oligocene of Colorado, the same genus being also represented in the Pleistocene of New Jersey, Pennsylvania and probably elsewhere in this country. Under the name of *Palæoperdix*, three species of fossil pheasants have been described from the Middle Miocene of Sansan (Gers). *Gallus* and *Phasianus* appear to be the only known Pliocene genera, but from the Pleistocene and cavern deposits of various parts of the world a considerable number of gallinaceous birds have been brought to light, the more important of which are enumerated in the following list.

Table Showing Geological Distribution of Gallinaceous Birds.

Middle Eocene.

Gallinuloides wyomingensis Eastman. Green River limestone; Uinta County, Wyoming.

Upper Eocene.

Palæortyx hoffmanni (Gervais). Gypsum of Paris Basin, Montmartre.
" *blanchardi* Milne-Edwards. Gypsum of Paris Basin, Montmartre.
" sp. indet. Gypsum of Paris Basin, Montmartre.
Filholornis paradoxa Milne-Edwards. Quercy Phosphorites.
" *gravis* " " " "
" *debilis* " " " "
Taoperdix pessieti (Gervais). Lacustrine limestone; Armissan (Aude).
" *keltica* Eastman. " " " "

Oligocene.

Meleagris antiquus Marsh. White River Beds; Colorado.

Lower Miocene.

Palæortyx cayluxensis Lydekker. Phosphorites of Caylux (Tarn-et-Garonne).
" *gallica* Milne-Edwards. Lacustrine deposits of Allier, and Phosphorites of Caylux.
" *brevipes* Milne-Edwards. Lacustrine deposits of Allier.
" (?) *phasianoides* " " " "
" *media* " " " " (*descrip. insuf.*).

Middle Miocene.

Palæortyx edwardsi Depéret. Saint-Alban-de-Roche (Isère).
Palæoperdix longipes Milne-Edwards. Sansan (Gers).
" *prisca* " " "
" (?) *sansaniensis* " " "
Phasianus altus " " " and Saint-Alban-de-Roche (Isère).
" *medius* " Sansan (Gers).
" *desnoyersi* " Orleannais.

Upper Miocene.

Phasianus altus Milne-Edwards. Lacustrine deposits; Œningen, Switzerland.

Lower Pliocene.

Phasianus archiaci Gaudry. Pikermi (Attica).
Gallus æsculapii " " "

Upper Pliocene.

Gallus bravardi Gervais. Ardé, near Issoire (Puy-de-Dôme).

Pleistocene.

Tetrao tetrix Linn. Kent's Hole Tavern, near Torquay, Devonshire.
" *urogallus* Linn. Forestbed (?) of Norfolk.
Lagopus albus (Gmelin). Cavern desposits near Montauban (Tarn-et-Garonne).
" *mutus* (Montin). " " " " "
Francolinus pictus (Jardine and Selby). Cavern deposits; Madras, India.
Coturnix novæ-zealandiæ Quoy and Gaimard. Superficial deposits; New Zealand.
Tympanuchus pallidicinctus Ridgway. " " Oregon.
Pediocætes phasianellus Linn. " " "
" *nanus* Shufeldt. " " "
" *lucasii* " " " "
Palæotetrix gilli " " " "
Meleagris superbus Cope. " " New Jersey.
" *celer* Marsh. " " "
" sp. indet. Caves of Pennsylvania.
Gallus sp. Rare in European bone caverns.
Perdix sp. " " " "

It will be seen from the foregoing that although gallinaceous birds are plentiful in the late Tertiary, with the exception of the Pliocene, our knowledge of them in the Eocene is confined to but four genera. Two of these, futhermore, are known by a solitary individual each; and as Eocene bird remains are seldom well preserved, it is clear that the discovery of fairly complete skeletons from this horizon is a matter of considerable interest and importance. The Carnegie Museum is therefore to be congratulated upon having recently acquired two tolerable skeletons of Eocene birds from the lacustrine limestone of Armissan, near Narbonne (Aude), the existence of which has not hitherto been made known.

These specimens form part of the famous Bayet Collection, presented by Mr. Andrew Carnegie to the Pittsburgh Museum in 1903; and through the unfailing courtesy of Dr. W. J. Holland, Director of the Museum, the present writer has been generously entrusted with their description. For this privilege he desires to express here his sincere thanks.

It has not been possible, however, to offer descriptions of both of these specimens in the following pages, owing to the fact that only one of them (fortunately the better preserved of the two) has not been sufficiently disengaged from the matrix to permit of its extended study. The specimen about to be described bears the Carnegie Museum catalogue number 2023, and belongs unquestionably to the genus *Taoperdix*, founded by Milne-Edwards[1] upon a unique individual from Armissan, which had been previously described by Gervais under the name of *Tetrao pessieti*.[2] Although agreeing with the type in its general characters, the Carnegie example differs from it in its greatly reduced length of wing, and in the disproportion of its limb bones; hence it may properly be regarded as constituting a distinct species. It may be fittingly designated as *Taoperdix keltica*, in commemoration of the name bestowed by Aristotle upon the inhabitants of the country near Narbonne.[3]

Taoperdix keltica, sp. nov. (Plates XIII.–XIV.)

Founded upon the crushed skeleton of a bird having approximately the size of a ruffed grouse (*Bonasa umbellus*), and differing from the type species of *Taoperdix* in the relative proportions of its limb bones, especially its much reduced humerus; also with shorter mandible. Upper Eocene; Armissan.

Although the skeleton is considerably dismembered and confused, both in the type of this species and in that of *T. pessieti*, as may be seen from a comparison of the plates, this circumstance must be regarded as rather fortunate than otherwise, since it permits of a more precise examination of the several parts. It is also fortunate that these two type-specimens should supplement each other in important respects. For our knowledge of the cranium we must depend solely upon the specimen belonging to the Carnegie Museum, although the mandible is present in both. Most of the limb bones, too, are better preserved in the new than in the older known species; but the latter, on the other hand, alone exhibits the furculum, sternum and pelvis in satisfactory manner. In the accompanying restoration of *T. keltica*, parts which are wanting or not clearly recognizable in the actual fossil are represented in outline after analogy with the type species or with recent pheasants, as the case may be. That is to say, when an epiphysis or articular condyle has become crushed or otherwise obliterated in the fossil before us, these parts are restored according to the usual conditions in modern *Phasianidæ*. All of the bones shown in Plates 1 and 2 are precisely as they occur in nature.

---

[1] Oiseaux Fossiles de la France, Vol. II., p. 225, pl. 127, Paris, 1871.

[2] *Comptes Rendus*, Vol. LIV. (1861), p. 896.

[3] Prior to the Roman conquest of Gaul, the whole of that country bore the name of Keltica; but after its occupation by the Romans the southern provinces were distinguished from the rest of Keltica by conferring upon them the name of *Gallia Narbonensis*. An interesting description of the Narbonnaise is given by Strabo in the fourth book of his *Geography*, and further accounts of this region are to be found in the well-known *History* of Polybius. Both of these ancient writers mention among the wonders of this country the occurrence of so-called "subterranean fish" or "dug mullets," which the inhabitants obtained by digging to a depth of two or three feet in marshy districts.

Passing now from these general considerations to an account of the several parts of the skeleton, we note that the head is of average size, rather abruptly truncated behind, with a maximum width of 2.2 cm. across the occiput, the orbits being rather posteriorly situated. The mandible is slender, without apparent downward curvature in front, approximately 3 cm. in length. The sternum and pelvis, not clearly indicated in the Carnegie example, but well shown in the type species, are regarded by Lydekker[1] as suggesting affinity with *Numidia* and *Meleagris*. It is an open question, however, whether the lateral aspect of the sternum has not become widened through mechanical compression of the matrix; at any rate the published figure creates a suspicion that such has been the case. A small portion only of the sacrum is preserved in the Carnegie specimen, the furcula is wanting, and the coracoids not distinctly reognizable. The last-named elements in *T. pessieti* are stout and straight, without subclavicular process, and with broad sternal facets. In both species the scapula is long and sabre-shaped, without being expanded posteriorly.

Important points of comparison are furnished by the limb bones, which are excellently preserved. It is evident that the species under discussion possessed but feeble powers of flight, the humerus being notably shorter than in *T. pessieti* and most living pheasants. This bone exhibits a slight double lateral curvature, and has a head of moderate size. The remaining wing bones are proportionally abbreviate, the brachium being of about equal length with the humerus. Nearly all of the bones of the manus in both wings are well preserved, and the same is true of the pes, The femur is relatively stout, of medium length, and with a slight forward curvature, the head being concealed. The tibio-tarsus is a stout bone, its length having a ratio of 1.3 as compared with the femur, and 1.7 as compared with the tarso-metatarsus. The latter element is without spurs, so far as indications show, and appears to have been more or less flattened from front to back. The trochleæ are of moderate size and widely separated. The phalangeals are slender and of medium length.

The relative length of the principal limb bones in this and other species is exhibited in this table, the tarso-metatarsus being taken as a standard of comparsion.

Species.	Tarso-metatarsus.	Tibio-tarsus.	Femur.	Humerus.
Taoperdix pessieti	100	174	130	143
" *keltica*	100	172	133	121
Palæortyx hoffmanni	100	172	124	141

The table given below is intended to facilitate comparison of the actual measurements of various bones of the skeleton in both species of *Taoperdix*. As there exists in some instances a discrepancy between the measurements given in the text of Milne-Edwards' work and those indicated in the plates, we have arranged the data obtained fron both sources in parallel columns.

---

[1] "Catalogue of Fossil Birds in the British Museum," p. 139 (London, 1891).

TABLE OF COMPARATIVE MEASUREMENTS.

Taoperdix keltica.		*Taoperdix pessieti.*	
Name of Parts.	Length.	Data from Text.	Data from Figure.
Tarso-metatarsus	3.3 cm.	3.5 cm.	3.7 cm.
Tibio-tarsus	5.7	6.2	6.3
Femur	4.4	4.6	5.0
Humerus	**3.7**	**5.0**	**5.2 and 4.8**
Ulna	3.6	4.8	4.8
Radius	3.3	(Wanting)	—
Metacarpus	2.0	2.5	2.5
Coracoid	(Incomplete)	3.4	3.4
Scapula	"		5.0
Mandible	**3.0**	—	**3.8**
Furcula	(Wanting)	—	3.8

No indications of plumage accompany either of the Armissan skeletons, although isolated feathers, and even egg-casts, are not uncommon in the lacustrine deposits of the south of France and in Switzerland. For references to the literature concerning detached feathers, one may consult an article on "Fossil Plumage," in the September number of the *American Naturalist* for 1904.

The following brief notice concerning the nature of the deposits at Aix and Armissan, together with their principal fossil contents, is sufficiently interesting to be reproduced in its entirety. It is taken from the second volume (pp. 551, 552) of Milne-Edwards' important work on the "Fossil Birds of France":

"Les marnes d'Aix (Bouches-du-Rhône), si riches en restes de Reptiles, de Poissons et d'Insectes, en empreintes de feuilles, etc., n'ont pas encore fourni d'ossements d'Oiseaux, mais on y a trové des œufs et des plumes admirablement conservés, dont quelques échantillons font partie du musée de Marseille. Ces marnes paraissent s'être déposées à la même époque que le gypse des environs de Paris. En 1836, M. Coquand y a trouvé des restes de Paléothérium, d'après lesquels il établit ce parallélisme qui ne fut pas adopté par Dufrénoy, mais que la plupart des géologues actuels s'accordent à admettre.

"C'est probablement aussi à la même époque que se sont déposés les calcaires lacustres d'Armissan (Aude), dans lesquels M. P. Gervais a fait connaître l'existence d'un Gallinacé, le *Tetrao Pessieti,* que j'ai étudié récemment et rangé dans un genre nouveau intermédiaire entre les Perdrix et les Paons, et que j'ai [re-]nommé *Taoperdix Pessieti.* Ces calcaires, toujours accompagnés de gypse, de rognons de soufre et de silex pyromaque, contiennent des débris de Paléothérium, d'Anoplothérium, des Reptiles, des Poissons d'eau douce, des Insectes, et une riche flore de végétaux qui paraissent avoir péri sous l'influence des causes qui ont agi à Aix."

Supplementary Note.

Since the above description was set in type, the task of working out the second bird skeleton (Cat. No. 2022), referred to above on page 134, has been skilfully performed by Mr. O. A. Peterson, one of the preparators of the Carnegie Museum. In its original condition many of the bones were only partially visible, and portions of them had been injured by the process of sawing or grinding to which the slab had been subjected prior to its acquisition by the Museum. As the result of Mr. Peterson's manipulation all of the preserved portions have been clearly exposed, thus permitting a far more accurate knowledge of details than could otherwise have been obtained. Fortunate as is this circumstance, it renders all the more conspicuous the fact that many characteristic portions, such as the articular extremities of several of the limb-bones, have been irretrievably lost through sawing the slab in two.[1] Notwithstanding the considerable injury done to the remains, they still furnish us with an important and very precious example of Eocene bird remains. The extreme rarity of complete individuals, not more than four or five being known from the Armissan deposits, increases the value of every item of information that is obtainable from any one of them. In the case of the present specimen, the loss of the head deprives us of perhaps the most significant information, concerning which we would have eagerly sought enlightenment. It remains for us to make as searching an inquiry as is possible from a decapitated body.

Fortunately we are able to satisfy ourselves in regard to a number of particulars with approximate accuracy. The conformation of the pelvis, typically gallinaceous, and the form and proportions of the limb-bones, all point to a very close relationship between this skeleton and the type species of *Taoperdix.* Indeed, it appears impossible to doubt that the present specimen and the type of *T. pessieti* are specifically identical, the differences between them falling well within the limits of individual variation. This conclusion is supported, in our judgment, by the following table of measurements, in which it has not been considered necessary to repeat the measurements of *T. keltica,* owing to their relatively greater disproportion. The same characters which enable us to discriminate between that species and the type compel us to distinguish between it and the second Carnegie skeleton now under discussion. A protographic reproduction of the new specimen (No. 2022), of slightly less than the natural size, is given in Plate XV. of this Memoir. In Plate XVI. several characteristic bones are shown as they occur in nature, except that in the case of the limb-bones, some of the articular extremities that have been injured are here partially restored.

---

[1] The specimen is evidently a piece of pavement slab, which was only discovered to contain fossil remains after it had been sawn. *Editor.*

TABLE OF MEASUREMENTS.

Type Specimen of *Taoperdix pessieti.*			Carnegie Example of Same Species.	Type Specimen of *Taoperdix pessieti.*			Carnegie Example of Same Species.
Name of Parts.	Data from Text.	Data from Figure.	Length.	Name of Parts.	Data from Text.	Data from Figure.	Length.
Tarso-metatarsus	3.5 cm.	3.7 cm.	4.2 cm.	Ulna	4.8 cm.	4.8	5.5
Tibio-tarsus	6.2	6.3	6.9	Metacarpus	2.5	2.5	2.8
Femur	4.6	5.0	5.0	Coracoid	3.4	3.4	3.7
Humerus	5.0	5.2 and 4.8	5.5	Scapula	—	5.0	5.0±

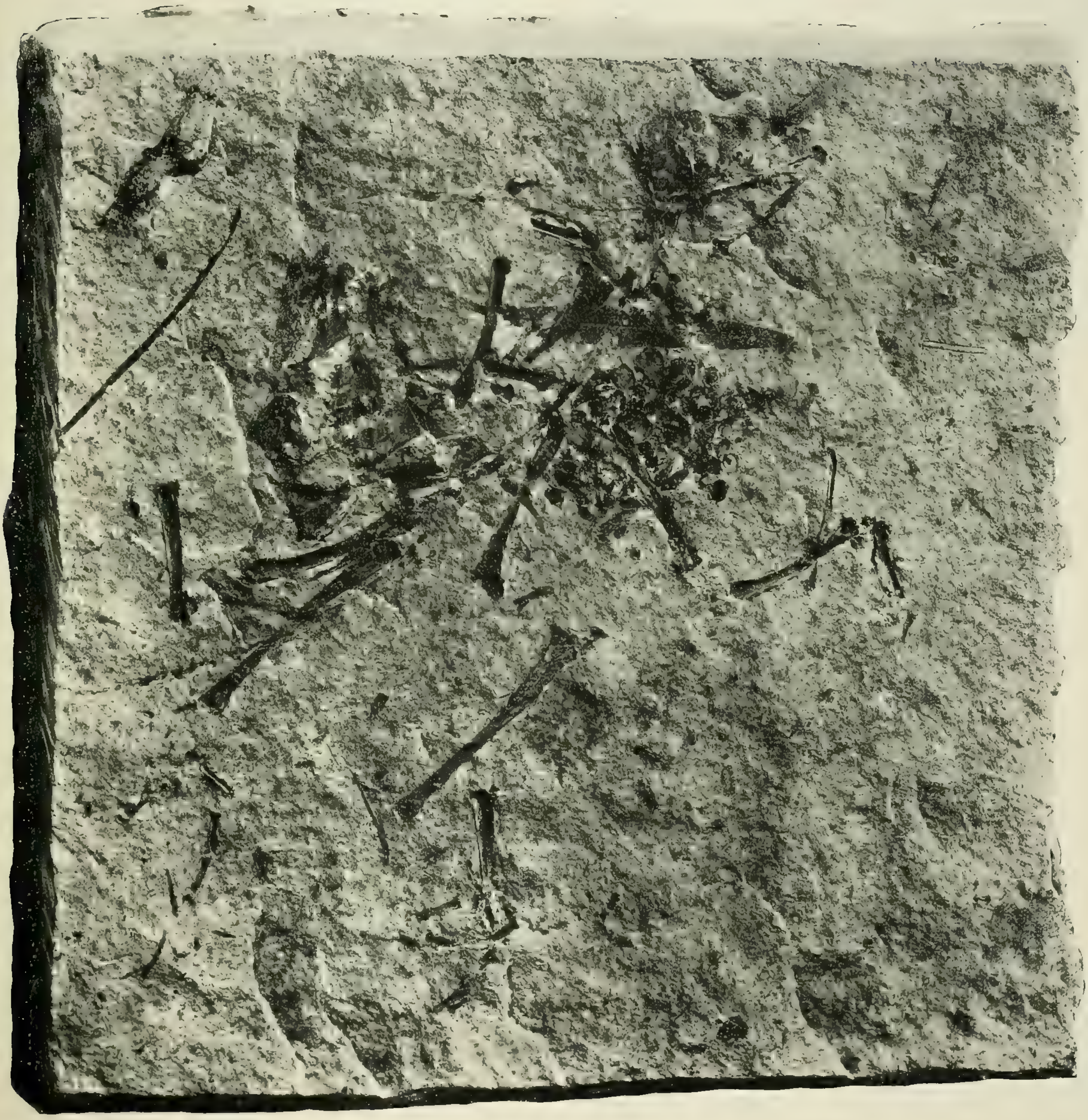
EXPLANATION OF PLATES.

PLATE XIII. *Taoperdix keltica,* sp. nov. Photograph of the specimen in its natural condition, × $\frac{1}{1}$.

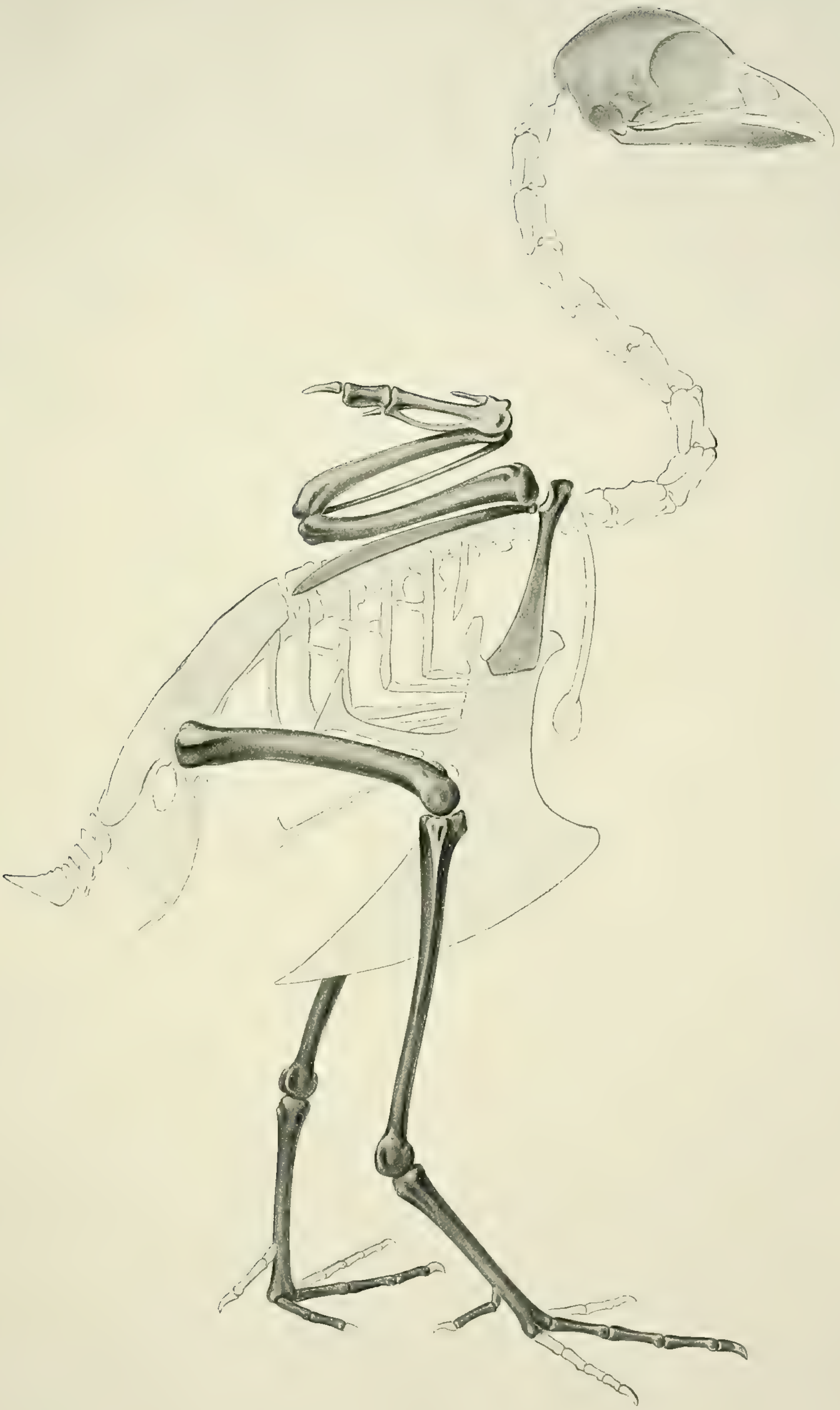
PLATE XIV. *Taoperdix keltica,* sp. nov. Restoration of skeleton, missing parts represented in outline, × $\frac{1}{1}$.

PLATE XV. *Taoperdix pessieti* (Gervais). Photograph of the second Carnegie specimen (Cat. No. 2022) in its natural condition, × $\frac{1}{1}$.

PLATE XVI. *Taoperdix pessieti* (Gervais). Illustrations of the more characteristic bones of the skeleton (Cat. No. 2022), some of the articular extremities slightly restored. All figures of the natural size. 1, *humerus;* 2, *radius and ulna;* 3, *metacarpus;* 4, *phalanges of pes;* 5, *tarso-metatarsus;* 6, *pelvis;* 7, *coracoid;* 8, *femur;* 9, *tibio-tarsus;* 10, *scapula.*

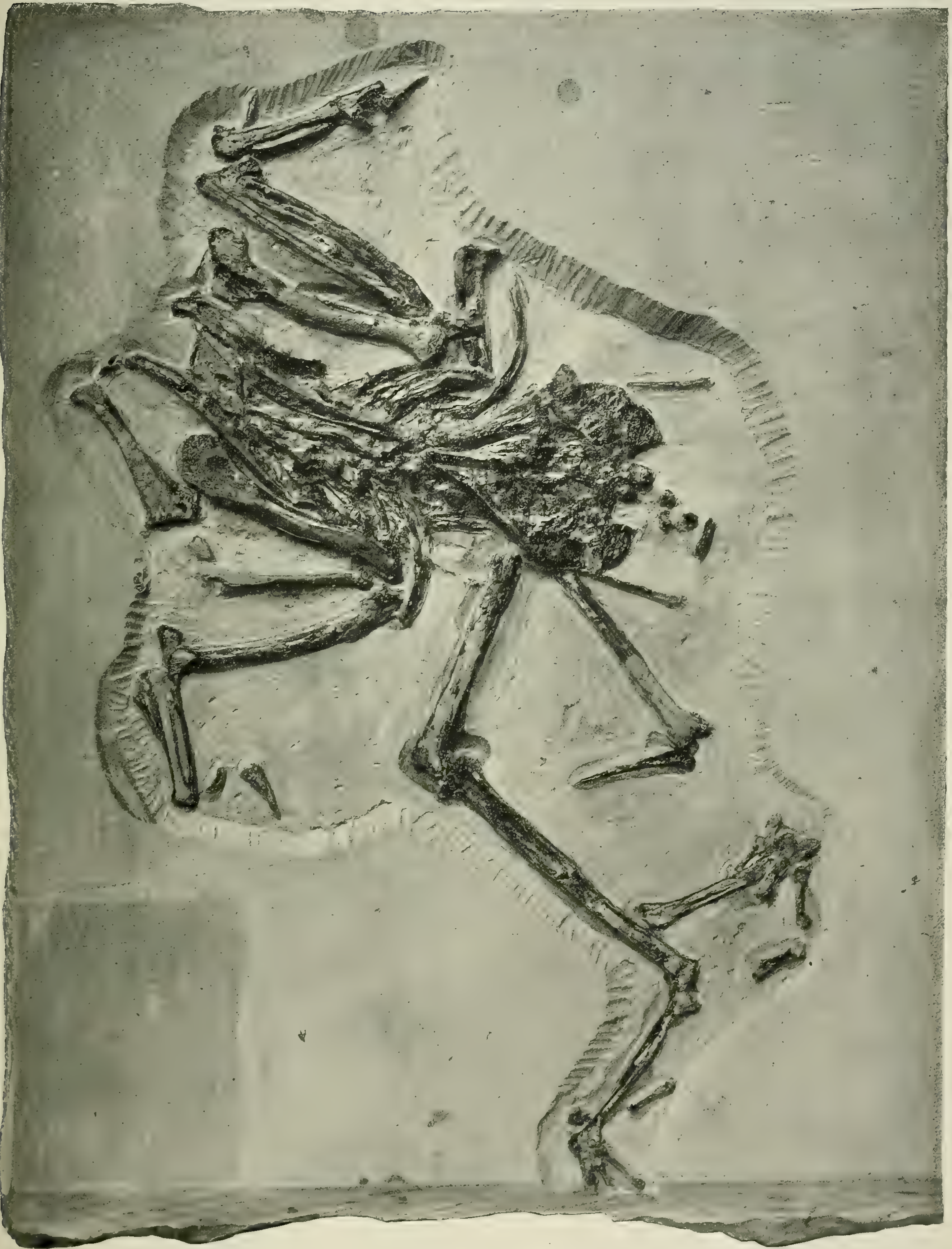


TAOPERDIX KELTICA EASTMAN. PHOTOGRAPH OF THE TYPE IN THE CARNEGIE MUSEUM.

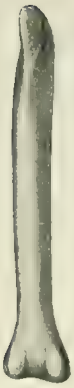


J. Henry Blake, del.

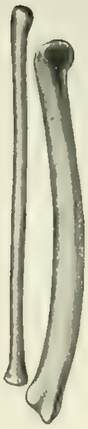
TAOPERDIX KELTICA EASTMAN. RESTORATION NATURAL SIZE. THE MISSING PARTS SUPPLIED IN OUTLINE.



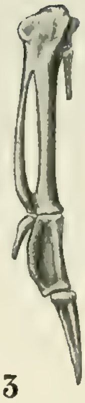
TAOPERDIX PESSIETI (GERVAIS). PHOTOGRAPH OF THE ORIGINAL IN THE CARNEGIE MUSEUM.



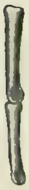
1



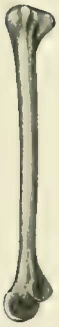
2



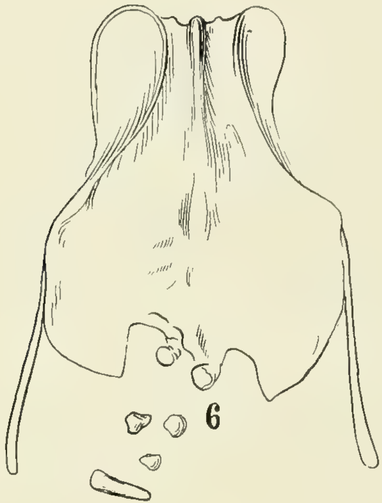
3



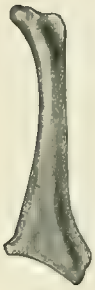
4



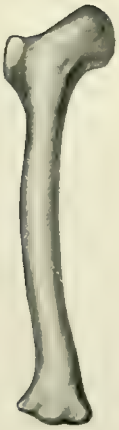
5



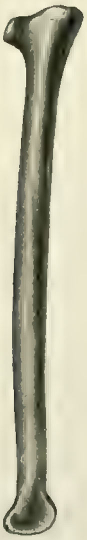
6



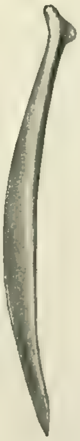
7



8



9



10

TAOPERDIX PESSIETI (GERVAIS).

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 4.

DESCRIPTION OF NEW RODENTS AND DISCUSSION OF THE ORIGIN OF DÆMONELIX.

BY O. A. PETERSON.

One of the field parties of the Carnegie Museum with the writer in charge was detailed by the Director to collect fossils in western Nebraska and eastern Wyoming during the season of 1904. In the collection which was secured are some very complete remains of rodents, belonging to two new species of *Steneofiber* not previously described. This material fully substantiates the views foreshadowed by Professor Scott, Dr. Matthew, and others, that this genus is clearly distinct from *Castor*. In the following detailed description of this new material it will be seen that there are some features, especially in the cranium, which are similar to those in the genus *Castor*, but these do not necessarily imply relationship. The skeleton as a whole shows osteological characters very similar to those of *Aplodontia rufa* with which I have compared it.[1] *Cynomys ludovicianus* is also used for comparison in studying the present fossil forms.

The material was discovered in the Upper Miocene sandstones, or Harrison (*Dæmonelix*) beds, in Sioux Co., northwestern Nebraska, and also in Converse Co., Wyoming, immediately across the Nebraska-Wyoming state line, and in the same general locality. Fossils are comparatively rare in this horizon. The list of genera found is as follows: *Promerycochœrus*, *? Mesoreodon*, a Peccary, *Oxydactylus*, and other small species of camels not identified. The commonest fossils from this horizon are the new species of rodents described in the following pages.

I take pleasure in acknowledging the valuable assistance of Mr. Earl Douglass in reading and correcting the manuscript and making kindly criticisms, of Mr. Sydney Prentice for making the drawings, of Mr. O. E. Jennings for working out the details in microscopic sections made from *Dæmonelix* and furnishing notes on his observations, of Mr. A. S. Coggeshall for photographs and of Mr. A. W. Vankirk for making the microscopic slides and assisting in cleaning up the material. To Director W. J. Holland is due special acknowledgment for the privilege of describing this interesting and complete material.

---

[1] A specimen of *Aplodontia rufa* (Col. U. S. Dept. Agri., No. 77975) was kindly furnished for comparison by Dr. C. H. Merriam, Smithsonian Institution, Washington, D. C.

Steneofiber fossor spec. nov.

This species is quite common in the Harrison (*Dæmonelix*) beds in eastern Wyoming and western Nebraska. This horizon immediately overlies the Monroe Creek beds and is probably equivalent to the upper John Day. There are fourteen specimens of this species in the Carnegie Museum collections, which were found inside of as many *Dæmonelices*. In some cases nearly complete skeletons were discovered. The type (No. 1217) was found near the rounded end of a "rhizome," and consists of the cranium, the vertebral column, including eleven caudals, (the extreme tip of the tail is missing), both clavicles, and a fairly complete set of ribs. The right and left fore limbs are complete, except the superior part of the right scapula and the feet. The pelvis and the posterior limbs are present, including the greater part of the right pes. No. 1208 is used as a cotype, and has the skull, lower jaws, eleven presacral vertebræ, the sacrum, both clavicles, the manubrium, and several ribs. The fore limbs are fairly well represented, and there are some fragments of the hind limbs. In the following description of the osteology of *S. fossor* use will be made of supplementary material, when, by so doing, additional light is thrown on the subject. In each instance the museum catalogue numbers will be referred to in connection with the specimens.

The Superior Dentition.

The superior incisors are comparatively as large and strong as those of the recent beaver; anteriorly the broad and flat surface is covered with a heavy coating of enamel, which forms rather sharp angular edges laterally. The rounded lateral and posterior faces have no enamel. The antero-posterior diameter is as great as the transverse. The chisel-shaped gnawing portions of the teeth are long and terminate anteriorly in a broad sharp edge.

The superior grinding teeth are rather small in comparison with the size of the skull. They gradually decrease in size from $p^{\underline{4}}$ to $m^{\underline{3}}$. Their position is nearly parallel with the long axis of the skull, and they are placed about midway between the anterior and posterior extremities of the skull.

P$^{\underline{4}}$ is the only superior check-tooth that retains the internal enamel-fold after the maturity of the animal. All the other teeth seem to have lost this character early, the surrounding enamel-bands showing no folding.

In the cotype (Pl. XVII., Fig. 3) there is a slight dissimilarity in the enamel pattern of the crowns of the premolars on opposite sides. The anterior fossette of the right premolar is oblong, and is the continuation of the internal enamel-fold, while on the tooth on the left side this fossette is smaller and rounded, and the anterior island is apparently independent of the internal enamel-fold. On the external enamel-band there remains a slight indication of the folding, which is shown only in the cotype in our series of skulls. There is also a small rounded fossette near the postero-external angle on both premolars, a character not found in the type.

Molar $^{\underline{1}}$ is broader than long in the cotype, while in the type its diameter is nearly equal in both directions giving it a subcylindrical form. There are three fossettes on the grinding face, one antero-external and transverse, the other antero-internal and oblique, while the third is a large fossette occupying an oblique position on the postero-external part of the tooth.

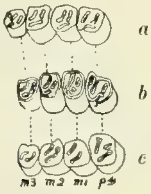


FIG. 1. Crown view of superior grinders of *Steneofiber fossor* representing different stages of wear. *a*, type, No. 1217; *b*, cotype, No. 1208; *c*, an old individual, No. 1207. Figures natural size.

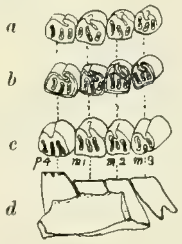


FIG. 2. Crown view of inferior grinders of *Steneofiber fossor*. *a*, type, No. 1217; *b*, cotype, No. 1208; *c*, an individual showing $p_{\overline{4}}$ in a nearly unworn stage; *d*, internal view of same specimen as *c*, No. 453. Figures natural size.

Molars $^{\underline{2}}$ and $^{\underline{3}}$. So far as the numbers and positions of the fossettes on molars $^{\underline{2}}$ and $^{\underline{3}}$ are concerned they are like the premolars. The last molar in the type is smaller than in any of the other skulls in the Carnegie Museum series.

THE INFERIOR DENTITION.

The inferior incisor is as large and as strong as the superior, and is similar to that of the recent beaver, excepting that in our fossil form, the anterior face of the tooth is flat. This is characteristic throughout the entire series. The left premolar is injured in the type, but the corresponding tooth on the right side is complete The anterior fossette is still connected with the enamel band, while that on the opposite tooth is free. This tooth ($p_{\overline{4}}$) has the three transverse fossettes and the external folding of the enamel usually seen in this genus. In *S. fossor* the folding of the enamel is somewhat similar in position, although not so deep as that in *S. montanus.* In *S. fossor* the tooth has a slightly greater antero-posterior diameter than $m_{\bar{1}}$. It has rounded anterior and posterior faces.

Molar 1. — With exception of the less rounded anterior face, and the deeper and more oblique external enamel-folding, this tooth is like the one in advance of it. In width and length the tooth has the same diameter.

Molar 2.—This tooth is similar to $M_{\bar{1}}$ with a slightly less transvere diameter. On the tooth in the left ramus the posterior fossette is divided in two portions, while that of the opposite tooth is undivided.

Molar 3. — The characters of the third molar are essentially those of the preceding molars 1 and 2. The tooth is smaller than those in advance of it. The teeth are quite prismatic, and terminate in short peg-like roots.

The Skull. Plate XVII., figs. 1, 2, 3.

The skull of *S. fossor* is comparatively large, with a rather low occiput, a low sagittal crest, moderately long muzzle, and broad zygomatic arches. In general outline the skull has a closer resemblance to that of *Aplodontia rufa*[1] than to any other recent rodent. In studying the skull in detail there are many striking differences between this and the recent genera. The nasals extend comparatively farther back than in *Aplodontia* or *Cynomys,* so that the fronto-premaxillary suture is more sinuous across the face and top of the skull than in these genera. Anteriorly the nasals terminate rather bluntly, not overhanging the premaxillaries. The lateral border of the nasal is supported entirely by the premaxillary, as in *Aplodontia.* They are broad and flat anteriorly, forming the roof of a triangular anterior narial opening.

The frontals are short, broad anteriorly, with a greatly constricted interorbital region. They terminate posteriorly in a wedge-shaped connection with the parietals. The supraorbital rugosity is quite heavy in some individuals of this species, and the temporal ridges take their origin at this swelling and rapidly unite opposite the interorbital constriction. There is no postorbital process on the frontal. In this respect the fossil is similar to *Aplodontia.*

In *S. fossor* the postorbital area of the frontal is more rounded than in *Aplodontia,* and the postorbital constriction is greater. There is a distinct sagittal crest in the type.

---

[1] The generic name first proposed in 1829 by Richardson was *Aplodontia,* and, while not satisfactory to a purist in Greek etymology, has priority, and must stand.—*Editor.*

The parietals extend well forward and overlap the posterior part of the frontals. Laterally, they unite with the squamosals by a suture, which runs antero-posteriorly in a parallel line with the long axis of the skull. Posteriorly the parietals are wing-shaped, on account of the large triangular interparietals. From the base of the sagittal crest each parietal is gently convex laterally. At the squamosal suture there is a slight swelling, the temporal region of the squamosal being more abruptly convex towards the zygomatic process than is the case in *Aplodontia.* The brain case is rather flat, but rapidly expands back of the supraorbital constriction.

The interparietal is large, and is like that of the recent beaver. In this region the skull bears a great resemblance to that of *Castor*, with a comparatively broader occiput, and straighter lambdoid crest. Posteriorly, the interparietals are broad, and they taper rapidly to an anterior point, thus occupying the V-shaped space in the postero-superior border of the parietals.

The occipital surface is almost vertical, as in *Cynomys*, but is much broader than in this genus. The supraoccipital occupies the greater portion of this area, as the mastoid is but slightly inflated. The entire surface superior to the foramen magnum is a vertical plane, and terminates superiorly in the lambdoid crest. Inferiorly there is a shallow emargination, which forms the superior border of the foramen magnum. At the point of contact with the exoccipitals in the lateral margin of the foramen magnum the suture extends outward and upward, and continues in an almost straight line to the junction of the mastoid and the posterior process of the squamosal. The sharp lambdoid crest takes its origin a little below this point, and continues in a gently curved line to the sagittal crest.

The occipital condyles are of moderate size and are not greatly separated by the emargination on the posterior face of the basioccipital. The paraoccipital process is small and points directly downward, terminating in a less truncated end than in the beaver. It is more nearly like that of *Aplodontia.* The occipital condyle is close to the otic bulla. The mastoid portion of the temporal bone is very little inflated. The mastoid process is broad laterally, and compressed antero-posteriorly, extending proportionally as low as that of *Castor.* It unites with the strong mastoid process of the squamosal, and is also fused together with the large external auditory meatus. This opening is somewhat like that of the beaver, the latter having a greater constriction just back of the opening of the tube. The whole region back of the zygomatic arches is short in *S. fossor*, and has a general resemblance to this region in *Aplodontia.* The tympanic bulla is inflated, flask-like, with a constricted but rather large tube, which is directed outward and upward, not horizontally outward as in *Aplodontia.* The position of the tympanic bulla is a character which very strongly recalls that of the recent beaver.

In the type (No. 1217) the base of the skull is damaged, but the cotype (No. 1208) supplements this region admirably. The basioccipital is entirely unlike that of the beaver, and is more nearly like that seen in *Aplodontia* and *Cynomys.* Anteriorly the basioccipital extends to opposite the anterior border of the otic bulla, in the type. In this region the inferior face has a slight shallow groove with two faintly indicated lateral ridges. These ridges meet 4 mm. back of the suture, and form a convex elevation, which increases in width posteriorly. In the beaver nearly the entire length and width of the basioccipital is deeply excavated inferiorly, which is a constant character. The presphenoid of the fossil is apparently similar to that of *Castor.*

The pterygoids are prominent and terminate in backward projecting alæ, which touch the otic bullæ. Superiorly, these hamular processes are emarginated, so as to form a large, oblong foramen, which leads into the large pterygoid fossa. The outer process bounding the pterygoid fossa extends back to the antero-external face of the otic bulla, and unites firmly with the floor of the brain case. The foramen ovale pierces this outer process of the pterygoid near the extreme inferior border. The alisphenoid cannot be outlined in either the type or cotype of this species. In skull No. 1212, however, the suture can be partly traced. The bone appears to be of large size, and similar to that of the beaver. The posterior wing extends to the tympanic, and forms a suture with it. The squamosal suture is immediately below the lower border of the glenoid cavity, and extends anteriorly in a sinuous line. The extreme anterior point cannot be ascertained, but may reach to the posterior border of the orbit. There is an alisphenoid canal.

The squamosal occupies relatively a greater area superiorly, than in the beaver. It has also a larger posterior portion, which joins the supraoccipital directly. In the beaver the parietal has a descending lobe postero-laterally, which unites with the mastoid portion of the squamosal. The squamosal is thus separated from the supraoccipital by this descending lobe in *Castor.* Anteriorly the squamosal extends relatively farther forward in *S. fossor* than in the beaver. The zygomatic process of the squamosal is similar in size, shape, and position to that of *Castor fiber.* Posterior to and continuous with the base of this process is a prominent and sharp border, like that in *S. peninsulatus,* which according to Cope, enlarges the postglenoid fossa more than in either *C. fiber* Linnaeus or *S. Eseri* v. Meyer (*S. viciacensis* Gervais). There is a subsquamosal foramen present in the type. The glenoid cavity is an antero-posteriorly elongated and laterally convex surface. The antero-posterior diameter is relatively greater than that of the beaver. The skull is broadest across the zygomatic processes of the squamosals.

The jugal is the most prominent bone in the zygomatic arch. The anterior process does not reach the lachrymal, and is proportionally shorter than in the beavers. There is a strong postorbital angle, similar to that in *Castor fiber*, *S. viciacensis* (see Cope, Tertiary Vertebrata, p. 841), and *S. peninsulatus.* The anterior part of the jugal, across the postorbital process to the inferior margin of the arch, is the widest surface of the bone. From this point backward, the jugal decreases rapidly, and terminates in a somewhat enlarged end, which forms the exterior border of the glenoid cavity. As a whole the zygomatic arch is proportionally wider and stronger than that of *Castor*, but otherwise is very similar.

The palatine plate of the maxillary extends posteriorly to the line between $m^{\underline{1}}$ and $m^{\underline{2}}$, and anteriorly to the posterior margin of the incisive foramina. In the beaver, the palatine plate of the maxilla is shorter posteriorly. In the type the posterior narial opening is well back of $m^{\underline{3}}$, and the front part of the palatine plate is much more concave than in *Castor.* Anterior to the alveolar border is a prominent ridge, extending from $p^{\underline{4}}$ in a curved line on the side of the muzzle, terminating abruptly below and in front of the infraorbital foramen. In the beaver, this ridge is not so prominently extended to $p^{\underline{4}}$; it is heaviest at the infraorbital foramen, and continues obliquely upward, across the maxillo-premaxillary suture nearly to the top of the skull, and unites with the malo-maxillary ridge forming a deep trough-like fissure for the masseter muscle. In *S. fossor* the malo-maxillary ridge extends forward only a short distance and does not join the upward extended ridge mentioned in the skull of *Castor.* In the type (No. 1217), the infraorbital foramen is small, which is characteristic of the genus. The zygomatic process of the maxillary is very strong, vertically broad, and ends abruptly at the inferior jugo-maxillary suture.

The lachrymal cannot be outlined in the type or cotype. In skull, No. 1207, however, this bone forms an extremely small part of the facial region. The bone is very small, perhaps even comparatively smaller than in the beaver, and, as in that genus, is located immediately internal to the opening of the lachrymal foramen.

The premaxillary is rather heavy to support the very large and powerful incisors. Below, it is laterally convex, with a median ridge extending from the incisive alveolar border to the anterior edge of the incisive foramen. The latter is relatively broader than in *Castor.* The maxillo-premaxillary suture in *S. fossor*, may be traced from the posterior border of the incisive foramen in a slightly curved line to the root of the zygomatic process, thence obliquely back to meet the fronto-nasal suture.

There is a strong swelling on the side of the muzzle, plainly indicating the direction of the root of the incisor. The muzzle is broadest across this swelling. The naso-premaxillary suture converges backward, making the nasals narrower posteriorly than anteriorly.

THE MANDIBLE. Plate XVII., figs. 1, 4.

The lower jaws are very heavy. The ascending ramus occupies more than half of the entire length of the mandible. The coronoid process takes its origin on the exterior side of the ramus, opposite the posterior part of $p_{\overline{4}}$; thence ascending in a gentle backward slope to near the summit, which is rapidly curved posteriorly, and terminates in a thin, rounded, and transversely compressed point. There is relatively a deeper and larger fossa separating the alveolar border from the coronoid process than in the beaver. In the fossil, the alveolar border is abruptly elevated above the diastema in front. Anteriorly, the jaws are united by a strong symphysis. On the chin is a strong process, similar to that in the beaver. The external face of the ramus is irregularly convex, the internal somewhat concave below the molar series. The angle is greatly deflected outward, and the inferior portion descends more below the border of the horizontal ramus than it does in the beaver. In *S. fossor* this angle terminates in a strong postero-lateral process. This process is very similar to that in *Aplodontia*, with somewhat less inferior and exterior development.

The alveolus of the incisor terminates posteriorly in a heavy, rounded protuberance on the external face of the ascending ramus below the condyle, similar to what is seen in *S. peninsulatus*. The deep fossa above this protuberance is similar in the two species, so far as can be judged from the type of *S. peninsulatus*. The form of the condyle also agrees with Cope's description: it "is subglobular, and has considerable more external than internal articular surface" (Tertiary Vertebrata).

With the exception of the less developed inferior process on the chin, the apparently more rounded anterior face of the incisor, the comparatively heavier femur and much longer tibia, the type of *S. peninsulatus* agrees closely with *S. fossor*. The skull, which Cope associates with the lower jaw, and the hind limbs of *S. peninsulatus*, figured on Plate 63, figs. 18, 18*a*, 18*b* (Tertiary Vertebrata), is distinctly different from *S. fossor* in having less expansion across the zygomatic arches, and possessing apparently a much shorter tube on the otic bulla, and a somewhat longer muzzle.

The skull figured and described as *S. pansus* (Bull. Am. Mus. Nat. Hist., Vol.

XX., pp. 257–270, 1904) has the same general shape as the skull of *S. fossor*, but the latter differs in having a relatively greater interorbital constriction; the diastema in front of the cheek-teeth is more highly arched; the palate is longer, and the basioccipital is not excavated. In *S. fossor* the ascending ramus of the mandible is not so vertical as that of *S. pansus*.

MEASUREMENTS.

Skull.

	Type.		Cotype.	
Greatest length	74	mm.	76	mm.
Greatest width	60	“	62	“
Greatest height, measured at m^3 to top of anterior part of sagittal crest	30	“		
Greatest width of occiput at external auditory meatus	48	“	48	“
Greatest width of muzzle anteriorly	12	“	15	“
Width of interorbital constriction	10	“		
Length of nasal	22	“		
Length of sagittal crest from union of temporal ridges to occiput	28	“		
Height of occiput	22	“		
Antero posterior diameter of otic bulla	13	“	13	“
Transverse diameter including tube and external auditory meatus			24	“
Extreme width of occipital condyles			16	“
Space between incisors and p^4	27	“	30	“
Space from m^3 to and including condyle			28	“
Width of palate at p^4	4	“	4	“
Width of palate at m^3			6	“

Superior Dentition.

Length of incisor from the alveolar border to the cutting point	21	“	21	“
Antero-posterior diameter of incisor	5	“	5	“
Transverse diameter of incisor	5	“	5	“
Antero-posterior diameter of grinding teeth	14	“	14	“
Antero-posterior diameter of p^4	4	“	4	“
Transverse diameter of p^4	4	“	4	“
Antero-posterior diameter of m^1	3	“	3	“
Transverse diameter of m^1	4	“	4	“
Antero-posterior diameter of m^2	3	“	3	“
Transverse diameter of m^2	3.5	“	3.5	“
Antero-posterior diameter of m^3	2.5	“	3	“
Transverse diameter of m^3	2.5	“	3	“

Mandible.

Greatest length of mandible including incisor	59	“	64	“
Length of mandible from process on angle to incisor—alveolar border	50	“	54	“
Greatest depth from angle to top of coronoid process	31	“		
Depth at diastema	10.5	“	12	“
	14.5	“	16	“
Height of coronoid process	9.5	“	9.5	“
Antero-posterior diameter of condyle	6	“	6	“

Transverse diameter of condyle	5	mm.	5	mm.
Length of diastema	16	"	16	"

Inferior Dentition.

Length of incisor from alveolar border to cutting point	25	"	27	"
Antero posterior diameter of incisor	5	"	6	"
Transverse diameter of incisor	4.5	"	4.5	"
Antero posterior diameter of grinding series	16	"	16	"
Antero-posterior diameter of $p_{\overline{4}}$	4.5	"	4.5	"
Transverse diameter of $p_{\overline{4}}$	4	"	4	"
Antero-posterior diameter of $m_{\overline{1}}$	4	"	4	"
Transverse diameter of $m_{\overline{1}}$	4	"	4	"
Antero-posterior diameter of $m_{\overline{2}}$	3.5	"	3 5	"
Transverse diameter of $m_{\overline{2}}$	4	"	4	"
Antero-posterior diameter of m_3	3	"	3.5	"
Transverse diameter of m_3	3.5	"	3.5	"

VERTEBRAL FORMULA. Plate XIX.

There were found, with the type (No. 1217), twenty-six presacral vertebræ, the sacrum, and eleven caudals. The vertebral column was not interlocked, vertebra with vertebra, when found, but it seems reasonable, that the following formula may be correct: seven cervicals, thirteen dorsals, six lumbars, five sacrals, and eighteen caudals, assuming that the last seven vertebræ are lost from the type. There are probably not more than seven or eight missing, to judge from the gradual tapering of the anterior caudal vertebræ, which were found in position and continuous with the posterior sacral vertebræ.

The Atlas. — The antero-posterior diameter of the atlas is smaller than that of *Aplodontia.* This is especially true of the superior arch. The inferior arch is a little heavier than in the latter genus. The articulation for the occipital condyle is very similar to that of *Aplodontia;* it is not very deep, and occupies, perhaps, more of the area of the anterior face of the atlas than is seen in *Aplodontia.* The foramen for the spinal nerve enters the superior arch internally, immediately above the cotylus, then pierces the arch to the superior face, and again reënters it in a postero-lateral direction. There are two posterior openings, one at the base of the transverse process on the lower side, and the other in the deep fissure above the articulation for the axis and at the base of the transverse process on the upper side. The foramen is similar to that of *Aplodontia,* but relatively smaller. In the type, the transverse process is complete, and is remarkable for its short and heavy character. The general aspect of the whole bone is similar to that of *Aplodontia.*

The Axis. — The axis is rather heavy, and is conspicuous on account of the high, strong, and antero-posteriorly broad neural spine, which overhangs the neural canal in front. Posteriorly, the neural arch overhangs the superior part of the short spinous process of the third cervical, so that the anterior part of the arch of the latter is entirely within the arch of the axis. In the cotype (No. 1208), the third cervical is entirely coössified with the axis (Pl. XVIII., Figs. 9, 9*a* and 9*b*.) The articulation for the atlas is extended well up upon the anterior border of the neural canal. The odontoid process is a heavy rounded peg. The delicate transverse processes are broken off on the axis and the third cervical.

The Third Cervical. — The third cervical is charactistic in *S. fossor*, on account of its tendency to become coössified with the axis. In the type, this vertebra is clearly separated from the axis, but the encroachment of the latter bone on the third cervical shows that in old individuals these two vertebræ may become coössified. In the type the neural spine is not so high as in *Aplodontia*, and the centrum has the same antero-posterior diameter as in that genus.

The Fourth Cervical. — This vertebra is represented by the centrum and half of the neural arch in the type specimen. The centrum is short antero-posteriorly, even shorter than the centrum of the third. Transversely, the centra are broad, and depressed vertically. The fourth cervical appears to have a heavier transverse process than in *Aplodontia.*

The Fifth Cervical. — The fifth cervical is almost identical in form with the fourth. The neural arch and spine are somewhat heavier than in *Aplodontia*, and the transverse processes appear stronger. The neural canal is large. The vertebrarterial canal is smaller than in *Aplodontia* and *Cynomys.* The prezygapophyses are directed forward and downward, and postzygapophyses upward and backward.

The Sixth Cervical. — The neural arch is injured, and the transverse processes of this vertebra are lost. The antero-posterior diameter of the centrum is less than in the preceding vertebra; otherwise there is not any marked difference between these two bones.

The Seventh Cervical. — The neural arch is low and broad, similar to that in *Aplodontia*, but heavier. The spine appears shorter. The antero-posterior diameter of the centrum is but very little greater than that of the preceding vertebræ. The transverse processes are heavy, and are directed horizontally outward from the centrum, not postero-laterally as is the case in all the preceding vertebræ. There is a distinct facet for the first rib on the posterior face of the centrum. This vertebra has no vertebrarterial canal.

As a whole, the cervical region is comparatively short and broad. With exception of the shape of the third cervical, the neck is similar to that of *Aplodontia.*

Dorsal Vertebræ. — There are thirteen dorsals more or less complete in the type specimen. The vertebra succeeding the thirteenth dorsal may or may not have supported a rib. This vertebra has no distinct transverse processes, and there are no visible facets for the ribs on the sides of the centrum. In view of the fact that *Cynomys* has apparently no distinct transverse processes on the first lumbar, I shall, in this description, regard the vertebra under discussion as the first lumbar.

The First Dorsal. — This vertebra has a less robust spine than is seen in *Aplodontia*, otherwise the neural arch is relatively as strong as in that genus. The short centrum has a plane surface inferiorly. The transverse processes are rather short and heavy, with a broad support for the tuberculum of the first ribs. The prezygapophyses are, as usual, placed low down on the arches, at the base of the transverse processes, while the postzygapophyses are higher up on the arch, in order to meet the articular surface of the succeeding vertebra.

The Second Dorsal. — This vertebra is complete with the exception of the tip of the neural spine. The latter is crushed to one side, which gives it a somewhat shorter appearance than the spine of the succeeding vertebra. The centrum is but slightly concave antero-posteriorly, and its diameter is very little greater than that of the first dorsal. The transverse process is strong, with a large tubercular facet for the second rib. The prezygapophysis is even lower down on the anterior border of the arch, than in the preceding vertebra, and does not extend so far beyond the arch anteriorly as in *Aplodontia* and *Cynomys*. The postzygapophysis is large and overhanging.

The Third Dorsal. — With the exception of a longer and somewhat stronger neural spine, and the shorter transverse process this vertebra is very similar to the one in advance of it.

The Fourth Dorsal. — The fourth dorsal is complete, except the top of the neural spine. The centra in this portion of the dorsal region gradually increase in length proceeding backwards; they decrease in their transverse diameter, increase in the vertical dimension, and acquire a more concave surface inferiorly. The fourth dorsal has strong transverse processes, which point outward and upward from their base. The rib contact is strong.

The Fifth, Sixth, Seventh, Eighth and Ninth dorsals are so similar that the description of one will answer for the entire series.

The neural spines gradually become lower, the transverse processes shorter, and the antero-posterior diameters of the centra greater. The inferior surface of the centrum is more convex fore and aft in the eighth and ninth than in any of the preceding dorsals. In these vertebræ, and the one in advance of them, the neural spines have lost their rounded form and gradually become laterally compressed. The tips of the neural spines of the sixth and seventh dorsals are broken off.

The Tenth Dorsal. — In the type, this vertebra is only represented by the neural spine, the prezygapophyses, and a small portion of the anterior part of the arch. This vertebra has the most delicate spine in the dorsal series.

The Eleventh Dorsal. — The eleventh dorsal is distinctly different from the preceding dorsals. This difference is chiefly found in the lateral convexity of the postzygapophyses, and in the presence of well developed metapophyses. The transverse process is only a small rounded knob, situated immediately below the base of the metapophysis on the exterior face of the pedicle. The spine of this vertebra is much higher than on the corresponding vertebra in either *Aplodontia* or *Cynomys.*

The Twelfth Dorsal. — There is no transverse process on this vertebra. The metapophysis is broken off. The neural spine is heavier, but is not so high as in the preceding vertebra. The postzygapophysis is more rounded than in the eleventh dorsal, and its articular face is directed more outward than downward. The centrum is less depressed than in the preceding vertebræ.

The Thirteenth Dorsal. — The right prezygapophysis and metapophysis are broken off from this vertebra in the type. The top of the neural spine is also injured. The centrum is much concave fore and aft, and is very little longer than that of the preceding vertebra. The large postzygapophysial articulation faces downward and outward, but is not as convex as that of the eleventh and twelfth dorsals. The strong metapophysis takes its origin at the base of the prezygapophysis on the superior part of the pedicle and terminates in a rounded point in a parallel line with the postzygapophysis. Its size, shape, and position are very similar to those of *Aplodontia* and the prairie-dog.

The change of direction of the neural spine occurs in the tenth dorsal in *Cynomys,* while this change of position is only slightly noticeable in the tenth and eleventh dorsals of *Aplodontia.* In *Steneofiber fossor* the change of direction of the neural spine is gradual, similar to that in *Aplodontia,* but it takes place in the twelfth and thirteenth dorsal (as in *Castor*), instead of the eleventh and twelfth. *S. fossor* also differs from *Aplodontia* and *Cynomys* in having higher spines on the posterior portion of the dorsal region.

The Lumbar Vertebræ. — The three anterior lumbars and the thirteenth dorsal were found articulated with one another by their zygapophyses. These vertebræ are complete except some of the delicate processes. As a whole, the lumbar region in *S. fossor* is more nearly similar to that of *Aplodontia* than to that of *Cynomys* or *Castor.*

The First Lumbar. — The first lumbar vertebra is decidedly heavier than the last dorsal. It is further characterized by the sudden increase of the antero-posterior diameter of the neural spine. If the last dorsal and the first lumbar had not been found in position, I would have been inclined to think that there might be a vertebra missing at this point. This vertebra resembles the preceding in not having a transverse process. Otherwise this bone is very similar to the following vertebra, which has all the characteristic features met with in this region. The inferior surface of the centrum is slightly keeled, and has a greater diameter antero-posteriorly than the last dorsal. The prezygapophysial articulation is a large surface, and is slightly concave.

The Second, Third, and Fourth Lumbars are so similar to one another that the description of one will answer for all. The antero-posterior diameter of the centra gradually increases; their inferior faces are more keeled; and the transverse processes become longer from the second to the fifth lumbar. The fourth lumbar has apparently no metapophysis. In this respect it is similar to the same vertebra in *Aplodontia.* The transverse processes are short and heavy, and are located on the pedicle, and not directly in contact with the centrum as in *Cynomys.* In *Castor,* these processes are high, but not as high comparatively as in *S. fossor* and *Aplodontia.*

The Fifth Lumbar. — This vertebra is represented by the complete neural arch, the centrum having apparently become absorbed by plants that are so common inside of *Dæmonelix.* The most characteristic feature of this vertebra is the sudden decrease of the neural spine. This is more apparent than in either *Cynomys* or *Aplodontia.* The transverse process is present on the left side, and is situated on a horizontal line with the postzygapophysis.

The Sixth Lumbar. — In the type, the left postzygapophysis and the end of the right transverse process are missing from this vertebra. The centrum has a greater antero-posterior diameter, and is more keeled than in any other presacral. The transverse process is prominent, and situated high as in the preceding lumbars. The neural spine is somewhat more reduced than that in *Aplodontia.* Otherwise this vertebra is very similar in these two genera.

The Sacrum. — There are five well coössified centra in the sacrum of *S. fossor.* In *Aplodontia* there are six, in a young *Cynomys* three, and in *Castor* four. In the cotype (No. 1208) there are five lumbar vertebræ and a sacrum; the last sacral is lost, but the centrum and the pleurapophyses on the preceding vertebra show, that there was coössification between the fourth and fifth sacrals. The number of sacral vertebræ in *S. fossor* consequently seems to be five, at least in two distinct cases. The centrum of the anterior sacral vertebra in the type (No. 1217) is very nearly as heavy as that in the last lumbar. The centra of the posterior sacrals rapidly decrease in size, corresponding to the moderately long tail.

The ilium is supported by the strong pleurapophyses of the three anterior sacrals. In the type specimen, the neural spines are all separated in a way similar to those in *Cynomys*. In the cotype, however, the first and second spines are coössified. In *Aplodontia*, the whole series back of the first spine is coalesced into a thin plate of bone, directed antero-posteriorly as also seems to be the case in *Castor*. In the type of *S. fossor*, the neural spine of the third sacral vertebra was injured during the process of cleaning up the specimen ; but the remains indicate, that it was perhaps the heaviest spine in the sacrum. The spinous processes on the two last sacrals are short, stout, and terminate in an enlarged rounded knob.

The sacrum as a whole presents the aspect of a narrow, long, and vertically deep column of bones. In *Aplodontia*, the sacrum is of approximately the same length, but has much less vertical depth, and decreases more rapidly toward the posterior end, than in *S. fossor*. The "Sewellel" has a remarkably short caudal region, while *S. fossor* has one about the length of that of *Cynomys*.

The Caudals. — As has been stated above, the tail of the type specimen consists of eleven anterior caudals. There were seven in a continuous series and in connection with the sacrum. The four remaining vertebræ are of about the right size to continue the series from seven to twelve. Assuming that the caudal series in *S. fossor* is similar to that of *Cynomys*, there would then be seven or eight vertebræ missing at the end of the tail.

The caudal region of *S. fossor* is heavier than in *Cynomys*, but in form it rather resembles the latter genus than *Castor* or *Aplodontia*. In the type the centra are short, round, and heavy. There is no neural canal back of the fourth caudal. The antero-posterior diameter is nearly equal in the first and last caudal vertebræ in the specimen under discussion. In the five anterior caudals there are distinct transverse processes. In *Cynomys*, these processes can be traced back to the ninth caudal, while in *Castor* they continue to the end of the tail. From the sixth caudal to the tenth, there are small protuberances on the inferior faces of the vertebræ, which may or may not have supported chevrons. In the Trans. Amer. Philos. Soc., vol. 17, 1893, p. 77, Professor Scott states that the anterior portion of the caudal region was provided with chevrons in *S. montanus*. The caudal vertebræ present in the type (No. 1217) indicate a heavy, moderately long, and round tail.

The Ribs. — *Steneofiber fossor* probably had thirteen pairs of ribs. *Cynomys* has twelve, *Aplodontia* fourteen, and *Castor canadensis* fifteen.

In the type specimen, there is a fairly complete set of ribs. The first is much flattened, expanded distally, and provided with a strong contact for the cartilaginous rib of the sternum. The shaft of the rib decreases in width superiorly, and is nearly round immediately below the heavy tuberculum. The head is rather small and rounded. The rib as a whole is different, especially distally, from that of *Cynomys* and *Aplodontia.* The latter genera have the lower end of the rib more rounded in cross section.

The ribs of the anterior half of the thorax are flat proximally, and rod-like distally. In the meso-thorax, and more posteriorly, they are rod-like throughout.

The Clavicle. — The clavicle in *S. fossor* is heavier than in either *Cynomys* or *Aplodontia.* In the cotype (No. 1208) both clavicles and the manubrium are present. The latter is much heavier than in *Aplodontia* or *Cynomys.* Anteriorly, there is a broad, gently rounded surface for the attachment of the clavicles. The attachments for the first set of ribs are very large, and are located close to the anterior end of the bone. Back of this rib-attachment is a long and gentle lateral constriction. Inferiorly, the bone is slightly keeled ; supero-anteriorly it is concave. Posteriorly it expands above and on the sides, indicating a rather large mesosternum.

Both clavicles in the type are complete, and are not so robust as those of the cotype. The latter specimen represents a somewhat larger and more robust individual. In shape, the clavicle is very similar to that of the beaver. The sternal attachment is more enlarged than in *Cynomys* and *Aplodontia.* The curve of the shaft in *S. fossor* is similar to that in *Aplodontia* and *Castor.* The superior end is less flattened than it is in the beaver and the prairie-dog, and does not terminate in an enlarged head as in *Aplodontia.* The clavicle of *S. fossor* gradually tapers from the large sternal contact to the superior end, which has on the internal face a wide, shallow groove at the contact with the acromion process of the scapula.

MEASUREMENTS.

Approximate length of the vertebral column including skull	37	cm.
Length of cervical region	20	mm.
Greatest antero-posterior diameter of atlas	6	"
Greatest transverse diameter of atlas	23	"
Greatest diameter of cotyli for occipital condyle	15	"
Greatest height of atlas	13	"
Antero-posterior diameter of centrum including odontoid process of axis	8	"
Antero-posterior diameter of centrum of axis at the base of the odontoid process	5	"
Greatest transverse diameter of axis anteriorly	12	"
Greatest height of axis including spine	16	"
Greatest height of neural spine of axis	6	"
Antero-posterior diameter of third cervical	3	"
" " " fourth "	3	"
" " " fifth "	3.5	"

Antero-posterior diameter of sixth cervical	3	mm.
“ “ “ seventh “	3	“
Length of dorsal region	72	“
Antero-posterior diameter of first dorsal	4	“
Transverse diameter of centrum of first dorsal, posteriorly	6.5	“
Height of centrum of first dorsal	3	“
Height including neural spine of first dorsal[1]	13	“
Antero-posterior diameter of centrum of fifth dorsal	5	“
Transverse “ “ “ “	7	“
Vertical “ “ “ “	3.5	“
Total height including spine on fifth dorsal	19	“
Total height of neural spine on fifth dorsal	12	“
Antero-posterior diameter of sixth dorsal	6	“
Transverse “ “ “	6 5	“
Height of centrum of sixth dorsal	4.5	“
Total height including spine on sixth dorsal	16 5	“
Antero-posterior diameter of centrum of twelfth dorsal	6	“
Transverse “ “ “ “	7.5	“
Vertical diameter of centrum of twelfth dorsal	5	“
Total height including spine on twelfth dorsal	15	“
Length of lumbar region	48	“
Antero-posterior diameter of centrum of first lumbar	7	“
Transverse “ “ “ “	7.5	“
Vertical “ “ “ “	5	“
Total height including spine of first lumbar	15	“
Antero-posterior diameter of centrum of third lumbar	8.5	“
Transverse diameter on posterior face of centrum of third lumbar	9	“
Vertical diameter of centrum of third lumbar	6.5	“
Total height including spine of third lumbar	16.5	“
Antero-posterior diameter of centrum of sixth lumbar	9	“
Transverse diameter of centrum of sixth lumbar, posteriorly	9	“
Vertical diameter of centrum of sixth lumbar	6	“
Total height of sixth lumbar including spine	14	“
Length of sacrum	36	“
Greatest width of sacrum, anteriorly	17	“
“ “ “ posteriorly	11	“
Antero-posterior diameter of first sacral	8.5	“
“ “ second “	8.5	“
“ “ third “	7.5	“
“ “ fourth “	7	“
“ “ fifth “	5.5	“
Height of sacrum anteriorly, including neural spine	16	“
“ “ posteriorly, “ “ “	10.5	“
Total length of eleven anterior caudals	73	“
Antero-posterior diameter of first caudal	6	“
Transverse “ “ “	4.5	“
Vertical “ “ “	4.5	“
Total height of first caudal, including spine	9	“

---

[1] The top end of the spine is broken off in the type.

Antero-posterior diameter of centrum of fourth caudal	6.5	mm.
Transverse diameter of centrum of fourth caudal	4.5	"
Vertical " " " "	4.5	"
Total height of fourth caudal, including tubercle	6	"
Antero-posterior diameter of centrum of eighth caudal	6.5	"
Transverse " " " "	4	"
Vertical " " " "	4	"
Antero-posterior " " eleventh "	5.5	"
Transverse " " " "	3	"
Vertical " " " "	3	"

The Fore-Limb. Pl. XVIII.

The left scapula in *Steneofiber fossor* is fairly complete in the type. In the cotype the scapula is complete, and this one is figured together with that of the type (see Pl. XVIII., fig. 2). This bone is conspicuous on account of the heavy and high spine. The lower border of the latter arises abruptly on the external face of the scapula 5 mm. above the glenoid cavity, then descends again in a curved line to form the very broad acromion process. This process extends much below the glenoid cavity. The spine forms a sinuous curve, and continues to the extreme superior border. It divides the narrow blade so as to form a slightly greater prescapular than postscapular fossa. The glenoid border forms almost a straight line from the glenoid cavity to the suprascapular border. There is no constricted neck above the glenoid cavity on the glenoid border. On a direct side view the spine is seen to greatly overhang the postscapular fossa. The latter is concave the entire length of the bone. The coracoid border of the scapula takes its origin at the base of the metacromion process, and continues in a curved line to within one fourth of the distance to the suprascapular border, where the blade is broadest; then it gently curves to the superior end. The superior half of the coracoid border is turned out so that it forms a concavity on the blade of the prescapular fossa. The suprascapular border is comparatively heavy. There is a heavy metacromion process, which is curved inward and backward. The glenoid cavity has an oblong antero-posterior articulation for the humerus, and is somewhat similar to that of *Aplodontia* and *Cynomys.* There is a neck on the scapula above the glenoid cavity on the coracoid border similar to that in the beaver. The internal surface of the blade, especially superiorly, forms an open, reëntrant, 3-shaped curve, like that seen in the beaver. The internal face of the scapula in *Cynomys* has sharp ridges running parallel with the long axis of the bone. This is also seen, in a less degree, in *Aplodontia.* These ridges are not sharp, and are gently curved in *Steneofiber fossor*, and are here more nearly like those in *Castor.* In fact, the bone as a whole, with the exception of the well developed metacromion, and the broad acromion process, is very similar to that of *Castor canadensis.*

The Humerus. — Both humeri are represented in the type as well as in the cotype. This bone (Pl. XVIII., fig. 3) is comparatively short and stout, and has a great lateral expansion distally. Proximally, the large head is well rounded, the antero-posterior diameter being the greatest. The tuberosities are fully as large as those of *Aplodontia.* The shaft is triangular in cross-section, especially so superiorly. The deltoid ridge is strong, with a transversely placed broad plate. This plate nearly equally overhangs the ulnar and radial sides of the deltoid ridge; it is entirely different from that in *Cynomys, Aplodontia,* or *Castor;* in the latter it has a large tuberosity on this ridge for the attachment of the deltoid muscle. In the type of *S. fossor* on the ulnar side below the tuberosity there is a short, sharp ridge, turned slightly posteriorly. As has been stated, the humerus is greatly expanded distally, the large internal epicondyle and the greatly expanded supinator ridge being the chief factors in this expansion. As in *Steneofiber montanus,* the supinator ridge extends high upon the posterior aspect of the shaft. The trochlea is relatively as broad and as shallow as that in the beaver. *Cynomys* has the trochlea much deeper, and *Aplodontia* has it about the same depth as *S. fossor.* The supratrochlear fossa is as deep or deeper than in *Aplodontia,* and the anconeal fossa is approximately the same as in that genus. The internal epicondyle is comparatively heavier than in the beaver, and is perforated by a large foramen, as in *S. montanus* and in *Aplodontia.* In the mole the internal epicondyle is relatively heavier than in *S. fossor,* and is perforated by a foramen.

Radius and Ulna. — The right and left radius and ulna are present in the type (Pl. XVIII., fig. 4, 4*a*). The forearm is relatively shorter than in *Cynomys* or *Aplodontia.* The shaft of the radius is a round and irregularly curved rod, and may be in somewhat closer proximity to the shaft of the ulna than is represented in our illustration. Superiorly the radius flares out abruptly into a large head to furnish a good support for the trochlea of the humerus. Distally the radius is even larger than proximally, and sends down a heavy internal and a smaller external process below the large articular facet for the carpals. In *S. fossor* this external process is much better developed than in *Cynomys, Aplodontia,* and the beaver.

The ulna has a heavier shaft than the radius; it is compressed laterally, and is broad antero-posteriorly, with a shallow groove extending from the sigmoid notch to near the distal end of the bone on the external side. This groove is better defined than in *Aplodontia,* which genus has the bones of the forearm in close contact throughout. In *Cynomys* the radius and ulna are separated, as in *S. fossor.* In the fossil the sigmoid notch is wide internally, with a strong supporting rib-like brace, which unites with the shaft below, and is relatively heavier than that seen in *Aplodontia.* The olecranon process is more produced upward, and has a stronger muscular attachment in *S. fossor* than in either *Cynomys* or *Aplodontia.* In the type the shaft of the ulna is much less curved than that of the radius, and terminates in a round knob, which articulates with the carpals.

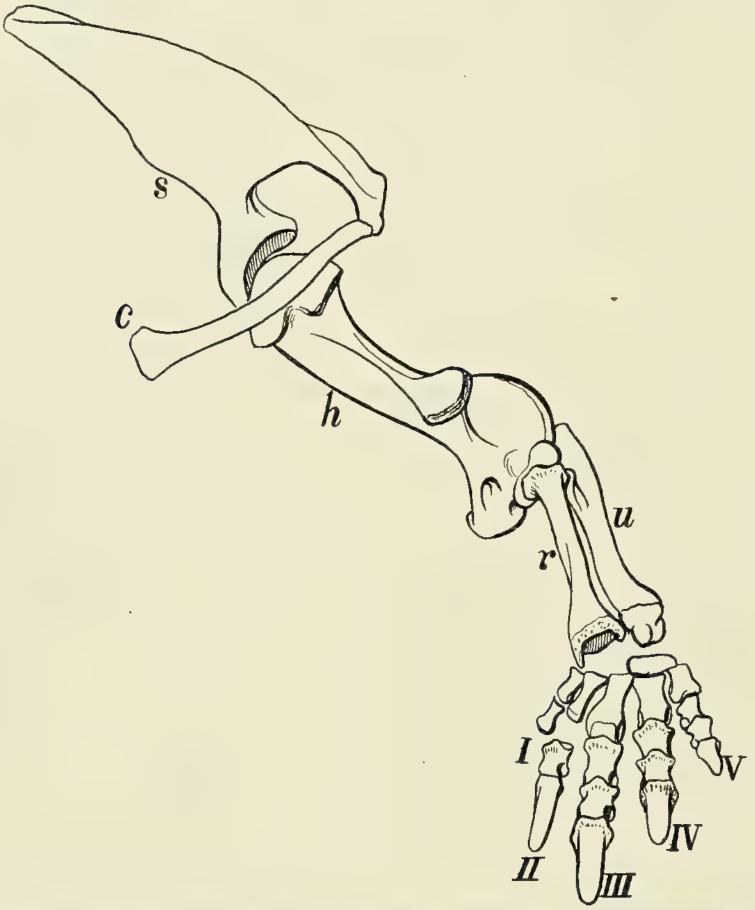


FIG. 3. Fore-limb of *Steneofiber fossor* in position ; somewhat larger than natural size.

The accompanying figure (Fig. 3) represents the fore-limb and foot of *S. fossor* in position. The limb presents a striking similarity to that of other fossorial rodents, and approaches that of the mole in its position. The elongated and narrow scapula of the mole, the heavy clavicle, the strongly built humerus, and the broad foot with the long and powerful unguals, is rather suggestive of the habits of this animal, which was probably fossorial to a considerable degree.

The Fore-foot. — Of the carpals there are, unfortunately, only the cuneiform, unciform, and trapezoid, the first and second metacarpals, and the first phalanx of the pollex represented in the type. Another individual of the same species, which is more robust (No. 1204) has the phalanges, first, second and third metacarpals, and the unciform preserved. A composite figure of the two specimens, the type, No. 1217 and No. 1204, represents the left manus of *S. fossor* on Pl. XVIII., fig. 5. The slight disparity of the two individuals is at once noticed in this illustration.

The Unciform in the type supports the fourth and fifth metacarpals. This bone is rather broad laterally, and the articulation for the scapholunar and cuneiform, is postero-radially a higher ridge than in *Aplodontia*, and is more nearly like that of *Cynomys*. Distally the articulation for the metacarpals is triangular in outline; it is concave fore and aft, and slightly convex transversely. The bone as a whole is similar to that in *Cynomys*.

The Trapezoid. — The trapezoid is a small irregular bone, which supports mc. II. The inferior articulation is obliquely concave antero-posteriorly. The superior surface is nearly flat.

Metacarpal I. — The first metacarpal is fairly well developed, and is parallel with the long axis of the manus. The first phalanx is strong, and supports an ungual, which is perhaps moderately developed as in *Cynomys*, *Aplodontia*, and other genera of this family. There is what appears to be a radial sesamoid in position in a smaller species. This species will be described later on in this paper.

Metacarpal II. is shorter than in *Aplodontia*, and is of about the same size.

Metacarpals III., IV., and V. are present in the specimen No. 1204, and are relatively short and heavy. Mc. III. is broken off superiorly, but it indicates a bone as long as the corresponding one in *Aplodontia*, and is much heavier. In the fossil, mc. III. is in comparison somewhat more expanded distally than that of *Aplodontia*. Mc. IV. is of the same length as that of *Aplodontia*, but is much heavier than in this genus or in *Cynomys*. In our fossil, the proximal articulation is deep antero-posteriorly. This is due to the large tuberosity on the plantar face of the bone. The shaft is slightly constricted, and the distal end has a strong keel on the palmar face.

Metacarpal V. is extremely short, has practically no shaft, and is as heavy as mc. IV. The articulations for the unciform and the proximal phalanx are quite large on the nodular-shaped bone. There is a deep transverse groove on the plantar face. The proximal row of phalanges are depressed and transversely broad. The proximal articulation is a rounded pit with a moderately deep notch on the inferior margin. The second row of phalanges are even more depressed than the proximal row. Proximally, the phalanges are concave antero-posteriorly and slightly convex transversely. The distal trochlea is broad, flat, and extends to a slight degree on the anterior face of the bone.

The ungual phalanges are heavy, long, and broad, with apparently no grooves anteriorly. The unguals have more similarity to those of the beaver than to those of *Cynomys* or of *Aplodontia*. Proximally, the unguals have a heavy plantar tuberosity. Distally the phalanges terminate in a sharp, depressed point. The plantar surface is broad and flat, and is entirely different from that of *Cynomys* and *Aplodontia*; it is more nearly similar to that of *Geomys*.

MEASUREMENTS.

Greatest length of scapula including metacromion process	45	mm.
Greatest width of scapula	16	"
Greatest height of spine of scapula	13	"
Length of acromion process	12	"
Antero-posterior diameter of glenoid cavity	9	"
Transverse diameter of glenoid cavity	5	"
Greatest length of humerus	41	"
Antero-posterior diameter of head of humerus	9	"
Transverse diameter of head of humerus	6.5	"
Greatest transverse diameter of distal end of humerus	16	"
Greatest length of radius	32.5	"
Transverse diameter of head of radius	5.5	"
Transverse diameter of distal end of radius	7	"
Greatest length of ulna	46	"
Height of olecranon process	10	"
Approximate length of manus	43	"
Height of unciform	* 3	"
Transverse diameter of unciform	* 5.5	"
Total length of metacarpal I	5	"
Total length of metacarpal II	8.5	"
Total length of metacarpal IV	* 9.5	"
Total length of metacarpal V	* 5	"
Length of ungual of fifth digit	* 6.5	"
Length of ungual of third digit	*13	"
Length of ungual of second digit	*10	"

* These measurements are taken from specimen No. 1204, which is a larger individual than the type.

THE HIND LIMB. Pl. XVIII.

The Pelvis. — The pelvis is well preserved in the type, and presents considerable similarity to that of *Castor canadensis*. The straight fore and aft diameter of the ilium and ischium, the heavy ischial tuberosity, and the wide posterior border of the thyroid foramen are especially similar in the two genera.

In *Steneofiber fossor*, the ilium is trihedral throughout its entire length. The supra-iliac border is not much expanded. The sacral surface is moderately long, and extends farther anteriorly than in *Cynomys* and *Aplodontia*. The external surface is a concave fossa nearly the entire length of the bone. The ischial border extends well back. The acetabular border is much more prominent than in *Cynomys* or *Aplodontia.* The pubic border is also quite prominent. The acetabulum is deeper than in the recent genera referred to; the ischium and pubis are stronger, and the thyroid foramen is smaller. The pubic symphysis is short, like that of *Aplodontia*, and a detached epiphysis was found in position in the type, similar to that of *Castor canadensis.* The vertical depth from the tuberosity on the ischium to the pubic symphysis is greater than in *Aplodontia* and *Cynomys.* The latter genera have the superior (anterior) part of the ilium turned outward (especially *Cynomys*) at a considerable angle, while *S. fossor* has not this feature. This is due to the greater anterior extension of the ilium, beyond the sacrum, and in order to give space for the posterior lumbar region in the recent genera; while in *S. fossor* the attachment for the sacrum extends more anteriorly, the last lumbar being opposite the supra-iliac border.

The Femur.—Both femora are well preserved in the type. This bone is somewhat more lightly constructed, and the neck below the head is longer than in *S. peninsulatus.* Otherwise the similarity is very apparent in the two species. In *S. fossor* the head is well rounded. The greater and third trochanters are relatively lighter, the whole bone longer, and not so flat as in the beaver. From Professor Scott's description ("The Mammalia of the Deep River Beds," p. 77) it appears that *S. montanus* has the third trochanter "placed more proximally than in *S. peninsulatus.*" In *S. fossor* the third trochanter is placed immediately above the middle of the shaft, as in *S. peninsulatus.* In *S. fossor* the fossa between the condyles is narrower and deeper than in *S. peninsulatus.* The condyles have the same relative proportion, and the trochlea are somewhat deeper than in the John Day species. In *Aplodontia*, the third trochanter is little developed, and is placed high up on the shaft like that in *Cynomys.* In *Castor*, the third trochanter is placed nearly midway between the proximal and the distal ends of the femur.

Patella.—The patella is present in the type, and its characters are nearly like those in *Cynomys* and *Aplodontia*, but different from those in *Castor*. In the latter genus, this bone is thick superiorly, and tapers to a trihedral point inferiorly, while in *S. fossor* it has a more ovate outline, and is as heavy below as above. The bone is larger than in *Cynomys* and *Aplodontia.*

The Tibia.—The tibia and fibula are well represented in the type, being present on both sides. The tibia is 4 mm. shorter than the femur. In the beaver, it is over 20 mm. longer than the femur. In *Fiber zibethicus* the tibia and fibula are also much longer than the femur. In the fossil, the relative length of the femur and the shin-bone is more nearly similar to that of *Cynomys* and *Aplodontia.* Proximally the articular surface has apparently a greater antero-posterior convexity, indicating perhaps a greater flexion of the limb than in *Cynomys* or *Aplodontia.* In the type the median eminence, or spine, is well developed, showing strong attachment for an intra-articular ligament. On the fibular side, near the edge of the articulation, there is a small sesamoid in position, similar to that seen in *Aplodontia* on the articular surface of the tibia. Proximally the shaft is strongly trihedral. The cnemial crest is as strong as in *Aplodontia* and *S. peninsulatus.* In the latter species, the tibia and the femur are of more nearly equal length than in *S. fossor.*[1]

Distally the shaft is more rounded in cross section. The astragalar facets have a somewhat greater antero-posterior diameter than in *Cynomys*, and the posterior downward process or malleolus is strong and not grooved as in the recent genus. The external articular facet for the astragalus is higher up on the bone, has an oblique position, and is much larger than the internal facet. There is a more distinct ridge separating these two facets in *S. fossor* than in *Cynomys.*

The Fibula. — The fibula is relatively as large as that of *Aplodontia* and *Cynomys*, and, as in these genera and the beaver, it is free. The proximal end is somewhat injured in the type, but it indicates a large tuberosity on the external side for the attachment of the lateral ligament, such as is found in *Aplodontia* and *Cynomys.* In *Castor*, this tuberosity is produced into a prominent process, directed downward and outward. In *Fiber zibethicus* this process is also quite prominent. The shaft of the fibula, in the type, is more flattened superiorly than in *Aplodontia*, and is more nearly like that in *Cynomys.* The distal epiphysis is slipped off so that its character cannot be ascertained. The calcaneum indicates, however, that the fibula may have touched the exterior face of the sustentacular facet.

The Tarsus. — The tarsus is represented in the type by the calcaneum, astragalus, cuboid, all the metatarsals, and the phalanges of the third and fourth digits. The second phalanx of the second digit is also present.

The tarsus and carpus of *S. fossor* have approximately the same relative size as in *Aplodontia* and *Cynomys*, and are entirely unlike those in *Castor*, as the following description will show.

Calcaneum. — The calcaneum in *S. fossor* has, as in *S. monianus*, "a short depressed, irregular, and club-shaped tuber." The tuber is relatively much broader than in the beaver, but the oblique exterior face seen in the latter genus, when the bone is in its position in the pes, is also very apparent in *S. fossor.* The articulation for the cuboid is a rounded, shallow pit. The sustentacular facet is relatively as broad as that in the beaver. As a whole, the calcaneum is perhaps more similar to that of *Castor* than to that of *Cynomys* or *Aplodontia*.

---

[1] Professor Cope's illustration ("Tertiary Vertebrata," Pl. 63, fig. 21) is incorrect. This illustration indicates a part of the shaft missing, but the true contact between the two parts has been found, and the bone fitted together, in the American Museum of Natural History.

Astragalus. — The principal difference, in the astragalus of *S. fossor* and *Castor*, is found in the prominent tuberosity below the articulation for the tibia, on the internal side near the sustentacular facet in the latter. This tuberosity is not present in *S. fossor*. *Cynomys* has it slightly indicated. In *Aplodontia* it is like that of *S. fossor*. In the latter, the constriction above the navicular facet, is relatively longer than in *Castor*, and is similar to that in *Cynomys*. The articulation for the tibia is regularly convex antero-posteriorly, and concave transversely, forming a rather shallow trochlea, similar to that in *Cynomys*. The navicular articulation is less spherical in the latter genus than in *S. fossor*.

The Cuboid. — The cuboid is injured antero-superiorly, so that the articular surface for the calcaneum is nearly lost, in the type. Judging, however, from the rounded, shallow pit on the distal end of the calcaneum, the facet on the cuboid would have a correspondingly convex, rounded appearance. In the beaver, the calcaneal articulation is a long, narrow, convex surface, which is placed obliquely antero-externally and postero-internally on the proximal face of the bone. The cuboid in the type has a more depressed appearance than in *Cynomys*, the distal end being more expanded, with a larger articulation for mt. IV., and no constriction above this facet on the posterior face of the bone, as in *Cynomys*. There is a strong contact for the ectocuneiform and the navicular.

Metatarsal I. — (Pl. XVIII., fig. 14.) The first metatarsal is somewhat more reduced in length than that of *Cynomys* and *Aplodontia*, and is not at all like the greatly developed hallux of the beaver. The digit is parallel with the long axis of the pes, as in *Cynomys* and *Aplodontia*. The proximal articulation is long and irregular antero-posteriorly, and narrow transversely. The ascending postero-external process, which reaches over and articulates with the plantar face of mt. II. in *Cynomys*, is represented only by a short rounded knob in *S. fossor;* it extends directly backward. The articulation for mt. II. is quite strong. The distal end is slightly enlarged, and the shaft consequently constricted ; the transverse diameter is a little greater than the antero-posterior.

Metatarsals II. and III., in the type, are of nearly equal length. Mt. II. has a narrow proximal articulation, and not an expanded head like that in *Cynomys*. The shaft is flat and depressed, distally enlarged, and has a heavy rounded plantar keel. The second digit in the beaver is comparatively lighter than in *S. fossor;* in *Cynomys* and *Aplodontia*, this condition is more nearly similar to that in the fossil. Mt. III. is the strongest metatarsal in the type; there is, however, not much difference in the metatarsals II., III., and IV., as is also the case in *Aplodontia* and *Cynomys*. The proximal articulation in mt. III. is slightly oblique, and extends to the posterior end of the plantar tuberosity. The shaft is broad, slightly constricted, depressed, and the distal articulation is moderately reflected on the anterior face of the bone. There is a strong keel.

Metatarsal IV. is slightly lighter than mt. III., in the type. In the beaver, this digit is a little the heaviest of the series. In the fossil the proximal end has somewhat similar interlocking characters with mt. III. and the cuboid, as in *Cynomys* and *Aplodontia*. These latter genera, especially *Cynomys*, have more rounded and much longer metatarsals than *S. fossor*. In *Aplodontia*, the metatarsals II., III. and IV. are approximately of the same length as those of *S. fossor*, but they are much lighter.

Metatarsal V. (Pl. XVIII., fig. 14) is only half as long as mt. IV. in the type. Its relative length is much less than in *Cynomys* or *Aplodontia*. In the beaver the fifth digit is relatively longer than in *Cynomys*. Metatarsal V. articulates with the outer side of mt. IV., and has no direct articulation for the cuboid. In *Cynomys* the superior end of mt. V. continues above the fourth metatarsal articulation in an upward and outward direction, terminating in a strong tuberosity. This tuberosity is developed in a much less degree in *Steneofiber fossor*, and is more like that of the beaver. The shaft of the bone in the fossil is short, constricted, and trihedral. The distal end is an enlarged, rounded knob, with distinct articulation for the first phalanx.

Phalanges. — The first and second row of phalanges are broad and depressed, similar to those in the manus. The articulation for the unguals is broad, plane, and well rounded on the anterior face of the bone. The unguals are somewhat smaller than on the fore foot, but of practically the same shape. The plantar rugosity is not so prominent as that of the manus.

MEASUREMENTS.

Greatest length of pelvis	66	mm.
Greatest width of superior border of ilium	11	“
Length of ilium from acetabulum to supra-iliac border	37	“
Length of ischium from posterior border of acetabulum to ischial tuberosity	23	“
Greatest width of ischium and pubis, posteriorly	26	“
Vertical diameter of ischium and pubis at symphysis, when pelvis is in position	15	“
Greatest length of femur	54	“
Transverse diameter of proximal end of femur	17.5	“
Transverse diameter of distal end of femur	13	“
Greatest length of tibia	51	“
Greatest antero-posterior diameter of tibia at proximal end	12	“

Transverse diameter of tibia at proximal end	12.5	mm.
Antero-posterior diameter of tibia at distal end	7	"
Transverse diameter of tibia at distal end	7	"
Greatest length of calcaneum	15	"
Length of tuberosity of calcaneum	7.5	"
Vertical diameter of tuberosity of calcaneum	7.5	"
Transverse diameter of tuberosity of calcaneum	4	"
Width of sustentacular facet of calcaneum	7	"
Greatest width of caclaneum at sustentacular facet	9.5	"
Greatest length of astragalus	10	"
Greatest width of astragalus	7	"
Antero-posterior diameter of cuboid	6	"
Transverse diameter of cuboid	4	"
Height of cuboid	4	"
Length of metatarsal I	10	"
Length of metatarsal II	14	"
Length of metatarsal III	15	"
Length of metatarsal IV	14	"
Length of metatarsal V	7	"
Length of ungual phalanx of fourth digit	9	"
Length of ungual phalanx of second digit (approximately)	10	"

Restoration of Steneofiber Fossor. Pl. XIX.

The type-specimen (No. 1217) is used as basis for this restoration. The scapula, however, and four of the anterior ribs in the illustration are drawn from the cotype (No. 1208). The greater portion of the fore-foot is reconstructed from the specimen No. 1204, which has also been referred to in the foregoing pages.

The articulated skeleton presents a number of interesting features. The most noticeable are: The cranium, which is unusually large in comparison with the body; the short neck; the long and narrow scapula; and the powerful limbs and feet. The thoracic cavity is quite large, equaling or perhaps exceeding, that of *Cynomys* or *Aplodontia.* The lumbar region is short and strongly built, as in *Aplodontia.* The pelvic region is even stronger than in either *Cynomys* or *Aplodontia,* and is in some respects more like that of *Castor.* The tail is round, rather heavy, and of moderate length.

The length of the fore limb of *S. fossor,* in comparison with the hind limb, is similar to that in *Cynomys, Aplodontia,* and *Castor.* The latter genera have the fore limb (the feet excluded) from 12 to 14 mm. longer than the hind limb; while *S. fossor* has the fore limb 10 mm. longer than the hind limb.

The skeleton of *S. fossor* has many features similar to those of *Cynomys* and *Geomys,* but, on the whole, it is perhaps more like *Aplodontia.* There are many cranial characters, together with the longer and broader ungual phalanges, and the much longer caudal region, which are very different from *Aplodontia.*

The specialization of certain parts of the skeleton of *S. fossor* conclusively proves that its ancestors had long been a divergent branch from the true forerunners of the family *Castoridæ.* At the present time I cannot confidentially point to any living rodent of which *Steneofiber fossor* might be the ancestor. That our fossil shows highly developed fossorial characters, is clearly evident from the study of the skeleton. It is plain that the beaver bears no close relation to it, so far as the structure of the limbs is concerned. The long fore-arm, the short femur, the long tibia, fibula, and pes, and the greatly developed hallux, in the beaver, are not suggested in *S. fossor.*

Steneofiber barbouri[1] spec. nov.

This species is founded upon the greater part of a skeleton, which is worked out in half relief (Fig. 4), and is still imbedded in its original matrix inside of a weathered "rhizome" of a *Dæmonelix.* It was found in the same horizon, and only a few hundred feet from where the type of *S. fossor* was discovered. To judge from Professor Cope's illustration ("Tertiary Vertebrata," Pl. LXIII., fig. 22), *S. barbouri* is of approximately the same size as *S. gradatus,* but differs from this species in having much more expanded zygomatic arches, more quadrate molars, larger tympanic bullæ and occipital condyles, and a much broader occiput.

The smaller size of the skull, and other characters, were at first regarded by the writer as individual variations, or possibly sexual differences only, which did not warrant a separation from *S. fossor.* However, a systematic study of the dentition and of the cranial characters has been made, which shows such marked differences from the preceding species, that a specific separation was deemed proper. So far as can be judged from the material at hand, the limbs and feet are apparently very little different from those of *S. fossor*, except that they are of smaller size. The

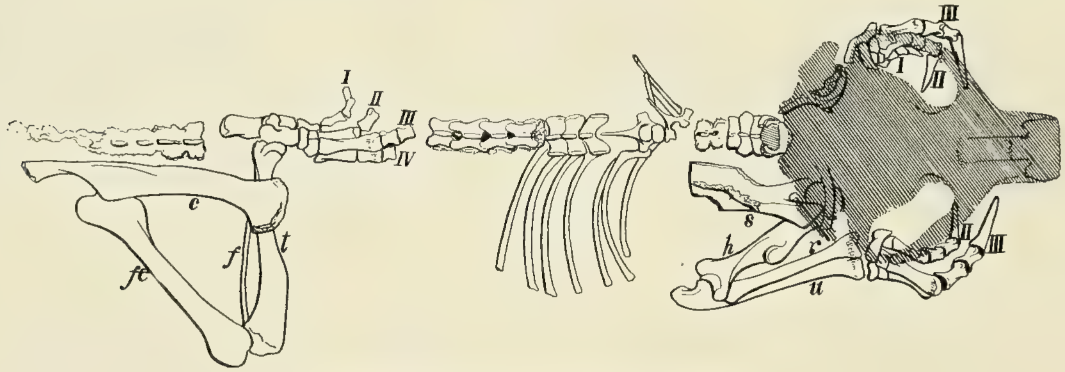


FIG. 4. *Steneofiber barbouri.* $\frac{3}{4}$ natural size.

---

[1] Named in honor of Professor Erwin H. Barbour, in recognition of his highly interesting work on *Dæmonelix.*

dentition and the cranium furnish good specific characters, by which *S. barbouri* may be distinguished from the species first described herein. They are as follows:

SUPERIOR DENTITION.

The superior incisor is relatively shorter, more curved, and more abruptly sharpened, with the anterior face somewhat more rounded, than in *S. fossor.* This tooth seems to agree more nearly with that indicated in *S. pansus* (*Bull. Am. Mus. Nat. Hist.*, Vol. XX., 1904, p. 250), than with that of *S. fossor.*

The cheek-teeth in *S. barbouri* have a relatively greater antero-posterior diameter in the skull than they have in *S. fossor,* but as in that species they are placed nearly parallel with the long axis of the cranium. The palate is also relatively broader in *S. barbouri.* Very little abrasion has taken place in $p\frac{4}{}$, so that the grinding surface of the tooth has not attained its greatest diameter. The internal enamel invaginations of all the superior cheek-teeth continue to the alveolar border of the maxilla. This is not the case in *S. fossor.* Molar $\frac{3}{}$ is triangular in section.

THE SKULL. Pl. XVII., Fig. 9; Pl. XVIII., Fig. 20.

While the general outline of the skull of *S. barbouri* is similar to that of *S. fossor,* a closer study reveals characters, which, besides the smaller size, distinguish it from that of *S. fossor.*

The distance from $p\frac{4}{}$ to the incisor is relatively a little less in *S. barbouri* than in *S. fossor.* The palatine area of the premaxillaries, in *S. barbouri,* is very little higher than the palate; while this region in *S. fossor* is greatly arched (see Pl. XVII., fig. 1, and Pl. XVIII., fig. 20). The interorbital space in *S. barbouri* is comparatively less constricted, and the temporal ridges are apparently less developed than in *S. fossor.* There may or may not have been a sagittal crest; the parietals are crushed down in the type, so that a positive statement regarding this cannot be made, until the discovery of more material. The anterior part of the zygomatic arch is relatively less robust, and the tympanic bulla larger than in *S. fossor.*

The contour of the skull of *S. barbouri* is not unlike that of the skull figured and described as *S. pansus* (in *Bull. Am. Mus. Nat. Hist.*, Vol. XX., 1904, p. 259). The excavated basioccipitals, (distinctly a character of *Castor*), the shorter palate, and the more vertical and higher ascending ramus of the mandible in the specimen in the American Museum, however, are clearly characters that distinguish it from *S. barbouri.* The latter species has the posterior nares back of $m\frac{3}{}$; the basioccipital is not excavated, and the ascending ramus of the mandible is at an angle similar to that in *S. fossor.*

The Mandible. — (Pl. XVIII., Figs. 18 and 19.) The inferior incisor has the relatively short appearance seen in the superior tooth. The external enamel folding extends well down on all the cheek-teeth. Premolar $_{\overline{4}}$, as in the upper series, is little worn, and presents two shallow internal, and one deep external enamel fold. The configuration of the crown is naturally more complicated. This would by further wear be changed. The first and second molars have about the same relative size as the tooth in advance of them, which is also the case in *S. fossor.* The last molar is proportionally somewhat smaller than in the latter species. The mandible as a whole is, excepting in size, identical with that of *S. fossor.*

MEASUREMENTS.

Greatest length of skull	50	mm.
Greatest width of skull	42	"
Width of muzzle	13	"
Width of interorbital constriction	11	"
Distance from incisor to p^4	16	"
Distance from $m^{\underline{3}}$ to occipital condyle	19	"
Width of palate at $p^{\underline{4}}$	4.5	"
Width of palate at $m^{\underline{3}}$	6	"
Antero-posterior diameter of tympanic bulla	11.5	"
Transverse diameter of tympanic bulla, not including constricted tube	10	"
Greatest transverse diameter of tympanic bulla including constricted tube	16	"
Transverse diameter of occipital condyle	13	"
Vertical diameter of occipital condyle	3.5	"

Superior dentition.

Antero-posterior diameter of incisor	3.5	"
Transverse diameter of incisor	3	"
Antero-posterior diameter of $p^{\underline{4}}$	2.5	"
Transverse diameter of p^4	2.5	"
Antero-posterior diameter of m^1	2.5	"
Transverse diameter of $m^{\underline{1}}$	2.5	"
Antero-posterior diameter of $m^{\underline{2}}$	2.5	"
Transverse diameter of m^2	2.5	"
Antero-posterior diameter of m^3	2	"
Transverse diameter of m^3	2.3	"

Mandible.

Greatest length of mandible	37	"
Greatest vertical diameter from coronoid process to inferior angle	21.5	"
Height of coronoid process	5	"
Vertical diameter of jaw in front of $p_{\overline{4}}$, including process on the chin	9.5	"
Vertical diameter of jaw at $p_{\overline{4}}$	10.5	"
Distance from incisor alveolus to $p_{\overline{4}}$	10	"
Distance from $m_{\overline{3}}$ to extreme back of angle	14.5	"

Inferior dentition.

Antero-posterior diameter of incisor	4	mm.
Transverse diameter of incisor	3	"
Antero-posterior diameter of $p_{\overline{4}}$	3.5	"
Transverse diameter of $p_{\overline{4}}$	3	"
Antero-posterior diameter of $m_{\overline{1}}$	3	"
Transverse diameter of $m_{\overline{1}}$	3	"
Antero-posterior diameter of $m_{\overline{2}}$	3	"
Transverse diameter of $m_{\overline{2}}$	2.5	"
Antero-posterior diameter of $m_{\overline{3}}$	2	"
Transverse diameter of $m_{\overline{3}}$	2.5	"

THE VERTEBRÆ.

The number of presacrals cannot be ascertained, since the type specimen is considerably damaged, in this region, by erosion. The cervical region is short, as in *S. fossor;* the dorsals are of approximately the same relative size, as well as the ribs and the lumbar vertebræ. The sacrum is almost entirely weathered away, so that its characters cannot be accurately determined. It was apparently long antero-posteriorly and narrow transversely. There remains only a faint indication of four or five proximal caudals, which were short, as in *S. fossor.*

The Clavicle is heavy, and is imbedded with the specimen in almost its natural position. In shape it is similar to that of *S. fossor.*

The Fore-Limb (Fig. 4) — The illustration represents the specimen in position, as it was found. The skull, lower jaws, the posterior portion of the dorsals, and the lumbars have been removed in order to show the characters of the feet. The left fore-foot is in position along the side of the skull. The rest of the limb is lost by weathering, as is also the left hind limb. The right fore-limb is nearly complete. The inferior portion of the scapula is preserved, and presents characters very like those of *S. fossor.* The humerus has also the strong deltoid ridge, that terminates in the transverse broad plate, which is seen in *S. fossor.* The transverse diameter of the distal end is much expanded. There is a large entepicondylar foramen. The radius and the ulna are relatively heavier than in *S. fossor,* but the length of the bone in comparison with the humerus is nearly the same in the two species.

Manus. — The fore feet in the type are practically complete. They are of approximately the same relative size as in *S. fossor.* In the carpus of *S. barbouri,* there are ten bones. The scapho-lunar bone is of the same size as that of *Cynomys.* The articulation for the radius is convex on the anterior part, and concave antero-posteriorly on the posterior part of the bone. In *Cynomys,* the whole proximal articulation is regularly convex antero-posteriorly. On the radial side of the manus in the type (No. 1210), there is a small compressed bone, which I take to be the radial sesamoid. The centrale is of the same size and shape as that in the manus of *Cynomys.*

Metacarpal III. is the longest of all the metacarpals; this is also true in the manus of *Cynomys, Aplodontia,* and other *Sciuromorphs.* The fifth metacarpal in *S. barbouri* is short and heavy, like that of *S. fossor.* The first digit in the type is parallel with the long axis of the foot, and supports a short, but well-formed ungual phalanx.

The ungual phalanges are, as in *S. fossor,* of unusually large size. Their shape is entirely different from that in *Cynomys* or *Aplodontia.* The latter genera have the unguals transversely compressed and high, while *S. barbouri* and *S. fossor* have them depressed and broad, suggesting the mole in this respect. The manus of *Geomys* has also similarities to that of *S. barbouri* and *S. fossor.*

The Hind-Limb. — Part of the pelvis and the left hind limb is preserved in the type of this species. The supra-iliac border of the pelvis is relatively broader, and has a more outward projecting hook in *S. barbouri,* than in *S. fossor.* In the type, the acetabular border of the ilium is sharp, and turns abruptly outward near the suprailiac border, forming the hook referred to above.

The Femur. — The head of the femur is in position in the acetabulum, and is apparently well rounded with a rather short neck. The great trochanter is quite strong, and the lesser trochanter is relatively as large as in *S. fossor.* The bone is injured in the region of the third trochanter. Distally, the femur is also imperfect. There is a weathered fragment of bone in the rotular groove, which is of about the right size to be the patella.

Tibia and Fibula. — The relative size of the tibia and fibula is approximately like that of *S. fossor.* In the type the delicate fibula is in position and is partially imbedded in the matrix. So far as can be judged from the view obtained, the fibula appears to be free as in *Cynomys, Aplodontia,* and the *Sciuromorphæ* in general.

The Pes. — The tuber of the calcaneum in the type is comparatively longer than in *S. fossor.* The pes as a whole has the same relative size to the manus as in *Aplodontia.* Unfortunately the pes is injured in the region of the phalanges. The proximal phalanx of the pollex is present, and its distal articulation indicates that there was a fairly large ungual phalanx. The proximal and median phalanges of the third digit are broad and depressed like those of *S. fossor.*

MEASUREMENTS.

Total length of the animal, approximately	25	cm.
Length of cervical region, approximately	12	mm.
Length of humerus	30	"

Transverse diameter of humerus, distally	13	mm.
Length of radius	25	"
Length of ulna, approximately	36	"
Length of manus, approximately	35	"
Length of metacarpal I	2.5	"
Length of matacarpal II	6	"
Length of metacarpal III	10	"
Length of metacarpal IV	7	"
Length of metacarpal V	4	"
Length of ungual phalanx of first digit	3.5	"
Length of ungual phalanx of second digit	8	"
Length of ungual phalanx of third digit	11	"
Length of ungual phalanx of fourth digit	8	"
Length of ungual phalanx of fifth digit	6	"
Length of ilium from acetabulum to suprailiac border	30	"
Transverse diameter of supra-iliac border	10	"
Length of femur, approximately	41	"
Transverse diameter of femur, proximal end	13	"
Transverse diameter of femur, distal end, approximately	11	"
Length of tibia, approximately	35	"
Length of tuber of calcaneum	6	"
Height of tarsal bones	10	"
Length of metatarsal I	5	"
Length of metatarsal II	9	"
Length of metatarsal III	12	"
Length of metatarsal IV	9	"
Length of metatarsal V., approximately	4.5	"

Probable Habits of Steneofiber Fossor and Steneofiber Barbouri.

Having carefully studied the remains of *Steneofiber fossor* and *barbouri* and compared them with recent fossorial and aquatic rodents, it is confidently believed that the two species under discussion belong to the fossorial kind.

That the remains have been found inside of *Dæmonelix* many times and in different localities, is an interesting fact well worth considering. If, therefore, it is assumed that *Dæmonelix* is the cast of the habitation of these terrestrial and fossorial animals, it becomes easy to explain the great numbers of *Dæmonelices* in certain localities. The extensive areas on the western plains, which are occupied by the highly gregarious genus *Cynomys* are well known. These animals and their underground tunnels offer a splendid example for comparison with what may prove to be the preserved records of the habitations of, at least, two species of the genus *Steneofiber*.

Nine species of *Steneofiber* have now been described from North America. I give here a synopsis of the characters, partially quoted from the original descriptions. In several instances, the types are so fragmentary that the specific characters are very few and unsatisfactory.

PRINCIPAL CHARACTERS OF THE NORTH AMERICAN SPECIES OF STENEOFIBER.

Steneofiber nebrascensis Leidy.

Pr. Ac. Nat. Sci. Philad., VIII., 1856, p. 88.

This species was found in the Bad Lands of White River, S. Dakota, in beds *C* and *D* of Dr. Hayden and Leidy's section. (The Extinct Mammalian Fauna of Dakota and Nebraska.) This horizon is perhaps equivalent to the Protoceras beds.[1] (See Matthew, Classification of the Freshwater Tertiary of the West. — Bull. Am. Mus. Nat. Hist., XII., 1899, pp. 19–75.)

This species is distinguishable by a small tympanic bulla, with the "external auditory passage forming a short oblique canal with its orifice directed outward and backward in the same manner" as in *S. viciacensis.* The angle of the lower jaw "is of less proportionate breadth than in the Beaver and is much bent inwardly. The condyle is higher or at a proportionately longer distance from the base. The single superior convexity" does not extend downward externally as in the Beaver (p. 339, Ext. Mamm. Faun.). Dr. Matthew (Bull. Am. Mus. Nat. Hist., XVI., 1902, p. 301–302) refers certain material in the American Museum collections from the Protoceras beds to Leidy's species, and further characterizes it as follows: "Long and narrow muzzle, small bullæ, sharp sagittal crest, and small braincase. The postorbital constriction is moderate, the pattern of the teeth rather complicated, two deep fossettes anterior to the external inflection on p^4 remaining in the well worn teeth of No. 1428." (This is the catalogue number of the specimen referred to *S. nebrascensis.*)

Steneofiber peninsulatus Cope.

Bull. U. S. Geol. Surv. Terr., VI., 1881, p. 370–373, and Tertiary Vertebrata, 1884, p. 840.

From the John Day formation (? Diceratherium beds), Oregon.

In the Revision of the *Mylagaulids*, Beavers, and Hares of the American Tertiary (Bull. Am. Mus. Nat. Hist., XVI., 1902, p. 291–310), Matthew defined this species as "more robust than the last [*S. nebrascensis*], distinguishable by the large bullæ and probably by the broader muzzle, wide occiput, larger brain-case and wider sagittal crest. The postorbital constriction is very narrow in the type, but not in the second specimen." (The latter character may indicate individual variation.)

The configuration of the cheek teeth in *Steneofiber* varies so much with age, that they do not furnish a reliable basis for specific determination. It seems, however, from figures by Cope and Matthew, that the superior grinders retain the enamel invaginations to a comparatively old age. The teeth are larger in comparison with the skull, than they are in *S. fossor.* The posterior narial opening is placed more anteriorly. The tympanic bulla is larger and more oblique, and "the meatal borders are produced into a short tube which is not so long as that of [*Castor*] *fiber*," and the zygomatic arch is less expanded. Cope says that the malar bone is "much expanded in a vertical direction, but has no postorbital angle, resembling in this respect the *S. viciacensis* rather than *C. fiber.*" The side view (Tert. Vert., Pl. LXIII., fig. 18) of Cope's illustrations shows a slight postorbital process.

---

[1] Wortman, *Bull. Am. Mus. Nat. Hist.*, V., 1893, pp. 101–102.

Steneofiber gradatus Cope.

(Paleontological Bulletin, No. 30, 1878, p. 1; Pr. Am. Philos. Soc., 1878, p. 63; Tertiary Vertebrata, pp. 844, 845.)

The type of this species, as that of *S. peninsulatus,* is from the John Day formation (Diceratherium beds?) of Oregon, and is much smaller. "The superior incisors are flat anteriorly, with external angle rounded, and its dentine presents the transverse undulation seen in *S. pansus.* . . . The middle line of the basioccipital bone is keeled, with a fossa on each side. The tympanic meatus is prolonged, and the post-tympanic process is short."

In the revision by Matthew, referred to above, the following characteristics of this species are given. "Short, wide muzzle, postorbital constriction moderate, brain-base short and rounded, temporal crests not uniting to form a single sagittal crest for some distance back of the postorbital constriction. Bullæ of moderate size; grinding series of teeth near together anteriorly, divergent posteriorly. The teeth decrease in size from $p^{\underline{4}}$ to $m^{\underline{3}}$ more than they do in *S. nebrascensis* or *S. peninsulatus;* there is but one fossette anterior to the external enamel inflection on the type, while our referred specimen of *S. nebrascensis* shows two, neither near extinction, although the teeth have attained the same stage of wear."

Steneofiber pansus Cope.

(Proc. Philad. Acad., 1874, p. 222; Ann. Rep. Chief of Engineers, 1875, II., p. 993; U. S. Geogr. Surv. West of 100th Meridian, Vol. IV., 1877, pp. 297–300).

The type of this species consists of fragments of two individuals associated. These were found in the Santa Fé Marls in New Mexico. The horizon is not satisfactorily determined. Dr. Matthews (Bull. Am. Mus., Vol. XX., 1904, p. 258), says: "We suspect from certain allusions in Professor Cope's descriptions that the type of *S. pansus* may also have been derived, along with '*Eumys*' *loxodon*, from similar[1] formation underlying the normal 'Loup Fork' (Upper Miocene) of New Mexico."

Regarding this genus "*Eumys*" *loxodon*, Cope says[2] that Dr. Hayden regards the Santa Fé Marls as late Tertiary, "but without special determination or coördination with other known lacustrine formations of this continent."

The fauna from this formation is, according to Cope, characteristically Loup Fork with the following list of genera: *Hippotherium, Protohippus, Procamelus, Cosoryx, Merychyus,* and known Pliocene species of other genera, among which may be mentioned *Canis, Aceratherium,* etc."

In the paper referred to,[2] Cope described a number of new species from the Santa Fé Marls, among which is (p. 150) *Hesperomys loxodon.* This "was found in the same deposits as the preceding species" which is *Cosoryx teres,* described on the same page (150).

In his later[3] publication, after having discussed *Stenofiber pansus,* Cope provisionally refers *Hesperomys loxodon* to "*Eumys*" *loxodon,* and quotes the original description in full, without regarding the fact that *Steneofiber pansus* and not *Cosoryx teres* is here the preceding species.[4]

In *Steneofiber pansus,* according to Cope, $p^{\underline{4}}$ of both series is conspicuously larger than the rest of the cheek teeth. The second and third molars are similar in proportions in *S. pansus.* From Cope's illustration it appears, that $p^{\underline{4}}$ retains the internal and external enamel inflections for a considerable length of time after the maturity of the animal. "The inferior incisors are almost quadrate in section, the two posterior angles being rounded. The enamel does not extend on either side, and is smooth; its transverse section is slightly convex. . . . The auditory bullæ are very large; they are subsemiglobular and compressed. The humerus preserved lacks epiphyses; its sections are triangular, owing to the presence of aliform angles. One proximal [angle] directed inward and backward is much more prominent than the deltoid crest opposite to it." The deltoid crest, then, is perhaps moderately prominent. The olecranon process of the ulna is short.

In Bull. Americ. Mus., Vol. XX., 1904, pp. 257–260, Dr. Matthew and Mr. Gidley describe a skull as *Steneofiber pansus* which was found in the lower Miocene of South Dakota. This may or may not be this species. It is distinctly separated from *S. fossor* by the moderately excavated basioccipital without the median ridge, and by the shorter palate, which "is roofed over as far back as the anterior border of the third true molar." In *S. fossor* the posterior narial opening is 4 mm. back of the third true molar.

---

[1] "Rosebud Beds," which, according to Matthew and Gidley, underly the true Loup Fork, and overly the White River on the Rosebud Reservation in South Dakota.

[2] *Proc. Philad. Acad.*, 1874, p. 147.

[3] U. S. Gogr. Surv., W. 100 Mer., IV., p. 300. 1877.

[4] This genus *Eumys* is perhaps not the true Oligocene genus, as it was found apparently in a much later horizon. Cope's description of the specimen is rather brief, and the figures given are unsatisfactory, so that without a study of the type nothing definite can be said regarding its relation to the genus from the Oreodon beds.

The ascending ramus of the mandible in the American Museum specimen is more vertical, and relatively higher than either in *S. peninsulatus*, *S. fossor* or *S. barbouri*. The specimen indicates an animal intermediate in size between *S. fossor* and *S. barbouri*.

STENEOFIBER MONTANUS Scott.

(Trans. Amer. Philos. Soc., Vol. XVII., 1893, pp. 76–78; Bull. Amer. Mus., Vol. XXI., 1902, pp. 303–304.)

Professor Scott writes me that the type of this species is lost. It was found in the Upper John Day beds of Smith River (Deep River), Montana.

"The incisors are narrow, with anterior faces which are less convex than in *Castor* and are covered with a thick layer of orange-colored enamel." "The caudal vertebræ indicate that this species had a longer and more slender tail than the beaver; the anterior portion was provided with chevron bones."

"The humerus has a rather slender, trihedral shaft and prominent deltoid ridge, which terminates in a massive, overhanging hook; this hook is proportionately even better developed than in *Castor*. The supinator ridge is also conspicuous and continues high up upon the posterior aspect of the shaft. . . . The internal epicondyle is very prominent, massive, and rugose, and is perforated by a large foramen."

"The femoral trochanters are well developed, but the third is placed more proximally than in *S. peninsulatus* or in the beaver." In *S. fossor* the third trochanter is like that of *S. peninsulatus*. "The calcaneum has a short, depressed, irregular, and club-shaped tuber; the sustentaculum is notably smaller than in the modern species, and the external projection near the distal end much more prominent; the cuboidal surface is of triangular outline and slightly concave." The third metatarsal is relatively very much more slender and shorter than in *Castor* and of different shape, as the shaft is of nearly uniform size throughout, not being contracted in the middle nor expanded distally; it is also more depressed and flattened, and the head for the first phalanx less enlarged. The proximal end has an oblique surface for the ectocuneiform, which is abruptly constricted behind and continued as a narrow posterior tongue."

The upper and lower teeth of the type are figured in the Bull. Amer. Mus., Vol.

XVI., 1902, p. 303. Matthew states that the type is "allied to *S. nebrascensis*, but larger, with somewhat longer teeth, and enamel inflections deeper and more complex. The type is an old individual, whence the antero-posterior direction of the internal upper and external lower enamel inflections on which Professor Scott largely relies to distinguish the species." The proximal position of the third trochanter on the femur, referred to above, may be considered as of specific value.

STENEOFIBER HESPERUS Douglas.

(Pr. Amer. Philos. Soc., Vol. XX., 1901, pp. 247–248; Bull. Amer. Mus., Vol. XVI., 1902, p. 304).

The type was found on Black Tail Deer Creek, about thirty miles above Dillon, in Beaverhead Co., Montana, in the Oligocene formation; the horizon not clearly determined by characteristic fossils.

The mandible is somewhat smaller than that of *S. pansus* of the Loup Fork of New Mexico. "The animal was not so robust as the New Mexico species." The masseteric area does not extend so far forward. "The anterior surface of the incisors is more convex than in the beaver, *Castor canadensis*, and the antero-posterior diameter is proportionally greater."

"The two anterior [lower] molars (m1 and m2) are broader and longer" than those in *S. pansus*. "The outer enamel inflections do not extend so far down on the outside of the teeth, are more open and incline more forward, and the outer lobes more angulate."

The type of this species is illustrated in Matthew's paper referred to above. In speaking of this specimen Matthew regards it as "close to *S. montanus*, if not identical; the difference in age prevents any accurate comparison. The size is the same at similar points of wear; the upper [should read lower: there are no upper teeth in the type] incisors are more rounded externally, but the value of this character is doubtful." The flat anterior face of the incisors in *S. fossor* is constant throughout the entire series of skulls and lower jaws in the Carnegie Museum collections, and is considered as of specific value.

The inferior premolars are the only basis for comparison in *S. montanus* and *hesperus*. The internal enamel folds are quite distinct on all the cheek teeth and the configuration of the triturating surface of $p_{\overline{4}}$ in *S. hesperus* is certainly more complex than in *S. montanus*. This is due in part to the younger age of *S. hesperus*. I give below the measurements of $p_{\overline{4}}$ taken from the author's descriptions:

Steneofiber montanus.	Length of lower molar ($p_{\overline{4}}$)	0.005	m.
	Width of lower molar ($p_{\overline{4}}$)	0.004	"
Steneofiber hesperus.	Length of $p_{\overline{4}}$ at base	0.005	"
	Width of $p_{\overline{4}}$ at base	0.0045	"

Steneofiber complexus Douglas.

(Pr. Amer. Philos. Soc., Vol. XX., 1901, p. 249; Bull. Amer. Mus., Vol. XVI., 1902, p. 304.)

The type was found in the Lower Madison Valley, about nine or ten miles south of Three Forks, Montana, in the Oligocene formation ; horizon not clearly defined.

The type is before me, and consists of a part of a skull and the lower jaws of a young individual. The temporal ridges apparently extended well backward before they united ; the muzzle is small and of considerable length. There is a long and gently curved diastema between the cheek teeth and the incisors; the latter are covered with heavy enamel anteriorly, and have a rounded face. "The masseteric area does not extend so far forward as in *S. hesperus*, and the anterior margin of the coronoid process rises opposite the back part of $m_{\overline{2}}$, and is nearer to the molar. This process has an entirely different form in this species. It is high ; the anterior border is straight and rises steeply. The angle is inflected inward and is rounded, not angulate anteriorly and posteriorly, as in *S. viciacensis*."

The anterior face of the lower incisor is not so convex as in *S. hesperus*, the posterior angle is broadly rounded. The outer part of the cutting edge is rounded, not angulate.

The upper cheek teeth are very complex, which is due to the small degree of attrition, the animal being young and retaining the milk premolars. Matthew regards most of the distinguishing characters given by Douglass as subject "to change with age and unsafe specific distinctions. The separate temporal crests may constitute a valid specific distinction." The vertical position of the ascending ramus of the mandible seems to suggest *S. pansus* as described by Matthew and Gidley, and is probably a valid character. When better material is found it may become necessary to unite *S. complexus* with *S. hesperus*.

Steneofiber fossor Peterson.

From the Upper Miocene, Harrison (*Dæmonelix*) beds, in Converse Co., Wyoming.

This species has rather small teeth in comparison with the skull ; muzzle and nasals moderately long ; zygomatic arches greatly expanded ; and there is a post-orbital angle on the jugal. Tympanic bulla inflated and flask-like, with a long, constricted tube, and a large external opening. Basioccipital not excavated, but slightly keeled. Palate extending well back of the third true molar. The palatine portion of the premaxillaries is greatly arched above the cheek teeth. Upper and lower incisors very strong with a flat anterior surface.

Cervical region short. A strong sacrum and pelvis; tail moderately long and round. Fore and hind limbs of nearly equal length. Feet broad, ungual phalanges depressed, broad and powerful. The animal robust, and with proportions similar to *Aplodontia* and *Cynomys*.

STENEOFIBER BARBOURI Peterson.

From the Upper Miocene, Harrison (*Dæmonelix*) beds, Converse Co., Wyoming.

This species and *S. gradatus* are of very nearly the same size. The muzzle in both species is short and wide; the postorbital constriction moderate, perhaps somewhat less constricted in *S. barbouri*. The brain-case in *S. barbouri* is moderately short. The temporal crests do not unite for some distance back of the postorbital constriction. The type specimen is crushed in this region. The injured parietals, however, show that the weakly developed temporal ridges were separated perhaps even farther back than in *S. gradatus*, and there may not have been a sagittal crest at all in *S. barbouri*. The superior grinding series in this species is more parallel with the long axis of the skull than is the case in *S. gradatus*. The width of the skull across the zygomatic processes of the squamosal is much greater (41 mm.) in *S. barbouri* than in *S. gradatus* (30 mm.). The latter measurement is taken from the illustration in the Tertiary Vertebrata, Pl. LXIII., figs. 22 and 22*a*. The same figures show that the transverse diameter across the skull at $p^{\underline{4}}$ is approximately 27 mm., while that of the Wyoming specimen is only 30 mm., giving the latter skull a greatly different, wedge-shaped, appearance (Pl. XVII., fig. 9). The basi-cranial region back of the molars in *S. barbouri* is shorter, the tympanic bulla and occipital condyles are larger, and the occiput is broader than in *S. gradatus*. The cheek teeth in the latter are decidedly less quadrate in outline, especially $m^{\underline{1}}$ and $m^{\underline{2}}$.

The general contour of the skull of *S. barbouri* is similar to the one described as *S. pansus* by Matthew and Gidley. The latter skull, however, differs in the excavated basioccipital, the shorter palate and the higher and more vertically placed ascending ramus of the mandible.

S. barbouri may be further characterized by the short neck, nearly equally long fore and hind limbs, broad feet, long and strong ungual phalanges as in *S. fossor*. In fact, the general make-up of the skeleton is similar to this latter species. It was, however, a smaller animal.

Euhapsis platyceps gen. & spec. nov.

Type, Plate XVII., Figs. 5, 6, 7, 8.

GENERIC CHARACTERS.

$P\frac{1}{1}\ m\frac{?2}{?2}$. *Teeth hypsodont. Premolar* $_{\overline{4}}$ *has the transverse diameter very nearly as great as the antero-posterior. The teeth in their worn condition have no external enamel inflections. The length of molars* $_{\overline{1}}$ *and* $_{\overline{2}}$ *together is very little greater than that of the preceding tooth* ($p_{\overline{4}}$). *The zygomatic arches are much expanded. The length and breadth of the skull is about equal. The occipital surface slopes forward. Parietals broad and short. No postorbital processes on the frontals. The tympanic bulla is inflated and flask-like. Basioccipitals not excavated, but slightly keeled. Mastoid processes directed outward, instead of downward.*

SPECIFIC CHARACTERS.

Incisors strong, somewhat trihedral in cross-section, anterior face very little rounded, and with a heavy band of enamel. Muzzle heavy and short. Infraorbital foramen small. Orbit irregular and high. Interorbital region moderately constricted. The space between incisor and $p^{\underline{4}}$ *on premaxillary very little arched. Basi-cranial region back of cheek-teeth short. Otic bulla with long and greatly constricted tube. Occiput low and broad. Two small foramina on either side of the median line of the basioccipital. Skull broad and depressed. Animal somewhat smaller than Aplodontia or Cynomys.*

The type (No. 1220) of this new genus and species consists of the skull and portions of both mandibular rami, and was found in the Upper Monroe Creek beds, near the head of Warbonnet Creek, Sioux Co., Nebraska. This horizon immediately underlies the Harrison (*Dæmonelix*) beds. The specimen was found close to a nearly complete skeleton of *? Mesoreodon*, and in the same sandstone ledge, where the four skeletons of *Promerycochœrus* were found, three of which are now on exhibition in the Carnegie Museum. In the same horizon were also found remains of small carnivores of the family *Canidæ*, small species of camels, and turtles, which are not yet identified.

The general outline of the skull presents similarities to that of *Mylagaulus monodon* (*Mem. Americ. Mus.*, 1901, pp. 377–379), and *Ceratogaulus rhinocerus* (*Bull. Americ. Mus.*, Vol. XVI., 1902, pp. 291–300). The extreme width of the cranium in comparison with its length, the wide and forward sloping occipital surface, and the general depressed appearance of the skull, are especially suggestive of the *Mylagaulidæ*. A detailed comparison, however, shows that the animal was perhaps more nearly related to *Steneofiber*.

The Superior Dentition.

Unfortunately, only the incisors are present in the skull. The grinders have all dropped out. The specimen is injured in the posterior part of the alveolar border and the region of the pterygoids. The superior incisors are nearly as strong relatively, as they are in *Steneofiber fossor*, and are of practically the same pattern : a nearly flat anterior surface, with heavy enamel. The gnawing surface is gradually worn down to a broad, thin, chisel-shaped point.

There are only two alveoli (for $p^{\underline{4}}$, $m^{\underline{1}}$) preserved on the left side of the maxillary ; the anterior one ($p^{\underline{4}}$) is smaller than the succeeding one, and does not appear —judging from its size — to have been occupied by a large tooth, such as is found in *Steneofiber.* On the right side, there is no alveole for $p^{\underline{4}}$, and on excavating this side of the maxilla, there was found no evidence of the presence of this tooth. This may be an accidental character of this particular individual, and may have no specific value.

The Inferior Dentition.

The inferior incisors are both broken off close to the roots, and there are three grinders in the left ramus. In cross-section, the incisors are subtriangular, similar to the upper incisors, with a broad, smooth, heavily enameled anterior face.

The premolar ($p_{\overline{4}}$) has very nearly twice the antero-posterior diameter of the succeeding tooth, which is contrary to what appears to have been the case with the corresponding teeth of the upper jaw, judging from the alveolus. The width of p_4 slightly exceeds that of the succeeding two molars. There are three irregularly placed enamel lakes on the grinding surface of $p_{\overline{4}}$; two of them antero-internal and transverse, the third oblique and postero-external. On the postero-internal enamel border there is a minute groove. This groove may be the remnant of the third internal enamel fold, as in *Steneofiber.* There is a slight evidence of the third enamel lake as in the latter genus, but in *E. platyceps* its greatest diameter is antero-posterior and it is not transversely placed.

The diameter of the first molar is one third greater transversely than antero-posteriorly. It has two enamel fossettes ; the anterior one is transverse, and appears to be the only remaining evidence of the internal enamel folding, the posterior one is curved and oblique, similar to that on $p_{\overline{4}}$. The second molar is similar to the first in every detail. There is apparently no alveolus for $m_{\overline{3}}$, and it is questionable if there was one. The root of the incisor is very close to the alveolar border in this region, so that, if the third molar had been present at any time, it must have been small, and must have had a weak support. The teeth have roots similar to those in the genus *Steneofiber.*

THE SKULL.

The general outline of the skull, as has already been stated, is suggestive of the *Mylagaulids.* It has, however, a number of characters similar to those of *Steneofiber fossor.* There are important characters, which probably, when the superior grinders are known, will show still more important generic diversity from *Steneofiber.* The skull — minus the nasals and the cheek-teeth — is excellently preserved, and deserves a somewhat detailed description.

The greatly expanded superior border of the premaxillaries indicates a broad rostrum, which in width exceeds that of the interorbital space, although not to the same degree as that which obtains in *S. fossor.* The nasals are comparatively broader than in *Steneofiber fossor,* but do not extend any farther posteriorly. About midway between the anterior and posterior ends, the nasals are broadest, then they gradually taper to a serrated, rounded point at the junction of the frontals. The fronto-premaxillary suture appears to be on a line with the posterior end of the nasals, as is the case in *Steneofiber, Cynomys,* and *Aplodontia.* Thus the nasals in *Euhapsis* are entirely supported laterally by the premaxillaries.

The frontals are rather short and broad anteriorly, with a heavy rounded supraorbital margin. The interorbital space is relatively as wide as that found in the family *Geomyidæ.* The posterior extension of the frontal is also somewhat similar to that in the latter family, with a slightly more pointed posterior process. There are no postorbital processes on the frontals.

The sutures in the posterior portion of the skull are not discernible, so that the forms of the separate bones of this region cannot be ascertained. The parietal is very wide, and necessarily short, on account of the forward slope of the occipital surface. The median line is indicated by low ridges, which nearly meet to form the low sagittal crest. The superior portion of the parietals have only a slight convexity from side to side, giving a broad and depressed appearance to the skull. The interparietal is not visible. The lambdoid crest, which takes its origin at the postero-external point (mastoid process) of the squamosal, is highly characteristic in this form. The extreme anterior slope of the occipital surface places the union of the lambdoid and sagittal crests forward one fourth of the total length of the skull. This forward slope is greater than in *Ceratogaulus rhinocerus* Matth. The latter has a slope of 30° from a vertical position (Bull. Amer. Mus., XVII., 1902, p. 293), while *Euhapsis platyceps* has a forward slope of about 55° from the posterior face of the occipital condyles to the top of the crest. The lambdoid crest is moderately high, but very sharp. The entire area of the occipital surface has a gentle convexity from the base of the condyles upward and outward to the top of the crest, presenting a comparatively plane surface. The transverse diameter of this surface is twice that of the vertical. The mastoid bullæ are only slightly inflated. The supraoccipital cannot be outlined by the suture, but is undoubtedly very large, to judge from the broad aspect of the skull in this region. The basioccipital is not excavated as in the beaver; it is somewhat triangular in shape, with two small perforations, one on each side of the median line opposite the posterior part of the tympanic bullæ. Postero-laterally from these perforations are the rather large condylar foramina. The occipital condyles are of moderate size, not very greatly separated inferiorly by the deep triangular notch; and they are farther separated from the tympanic bulla than in *Steneofiber fossor.* The foramen magnum is of large size and subtriangular in shape. The mastoid process is of medium size, and has a unique outward and horizontal position, similar to that in *Aplodontia,* but is more rounded. The long, constricted tube of the auditory bulla is supported by the mastoid process nearly to its outer portion — the external auditory meatus. The latter opening is broken away in our specimen, but was perhaps not of great size to judge from the greatly constricted tube. The tympanic bulla is much inflated, chiefly laterally and antero-posteriorly; it is depressed vertically, and takes up a considerable area of the basicranial surface. The shape of the bulla is flask-like, with an unusually long and much more constricted neck than in *Aplodontia.* The genus *Entoptychus* from the John Day Miocene has the constricted neck of the bulla; but the general features of the skull in *Euhapsis* are entirely different from it, and bear a more general resemblance to *Steneofiber.*

The Squamosal has a considerable posterior process, which unites with the base of the mastoid process from which the lambdoid crest takes its origin. In front of this process, and immediately behind the zygomatic process of the squamosal is a deep rounded emargination (the postglenoid notch), similar to that in *Steneofiber, Entoptychus,* and the recent genus *Aplodontia* and the *Geomyidæ.* In *Euhapsis platyceps* the zygomatic process of the squamosal is of small size and rather short; the jugal and zygomatic process of the maxillary furnishing the greater part of the arch.

There is an obtuse, round, postorbital swelling, from which continues latero-inferiorly a sinuous ridge, which is continuous with the anterior margin of the zygomatic process. The glenoid cavity is not as distinctly formed as in *Fiber zibethicus,* and indicates a considerarable lateral motion of the mandible. The anterior border of the squamosal cannot be accurately determined, since the suture is obliterated at the posterior margin of the orbit. The parieto-squamosal suture is much lower down on the side of the skull than in *Steneofiber fossor.*

In the region of the sphenoid bones the skull is damaged. The basisphenoid appears to be crowded especially posteriorly, where the tympanic bulla is encroaching upon it. The posterior part of the basisphenoid sends a backward projecting process on either side of the median line. These processes are fused with the internal face of the otic bullæ, and extend to a considerable distance back on these bones. The pterygoid fossa is quite large, and the external wing of the pterygoid seems to have reached well back, and is fused with the floor of the brain-case very close to the antero-external face of the tympanic bulla. The foramina, ovale and rotundum, seem to be coalescent, as in *Aplodontia.*

The Jugal is nearly vertical anteriorly, and is a comparatively heavy plate of bone. In shape and size it is very nearly like that of *Castor*, the vertical portion just back of the orbit being comparatively deeper than in the recent genus. At the extreme inferior jugo-maxillary suture, the arch forms a heavy, rounded, tubercle-like angle. At the supero-anterior portion the suture is not distinct, but I would judge that the jugal forms a suture with the lachrymal; the suture of the latter bone is also indistinct. There is a large lachrymal foramen in the orbit, similar to that of *Castor.*

The greatest width of the skull is obtained across the posterior part of the jugal. The extraordinary width and strength of the zygomatic arch is one of the principal characters of the skull, and recalls such recent forms as the *Geomyidæ* and *Aplodontia*, and also the Loup Fork *Mylagaulids.*

The postorbital process on the jugal is fairly well developed in *Euhapsis platyceps.* The orbit is imperfectly rounded, and is placed high.

The Maxillary. — The zygomatic arch of the maxillary is very similar to that of *Castor*, but arises more posteriorly on the maxillary (opposite $\mathrm{m}\frac{1}{}$), than in the beaver (opposite $\mathrm{p}\frac{4}{}$). The infraorbital foramen is small and almost entirely hidden by a vertical ridge or projection from the maxillary like that in *Castor.* In fact the skull in this region resembles the recent beavers, with the exception of the much more produced angle at the inferior jugo-maxillary union on the zygomatic arch.

The Premaxillaries. — The premaxillaries are broad, short, and heavy. Inferiorly the palatal surface is comparatively broad and has not the long, gentle, and concave antero-posterior sweep between the alveolar border of the maxillaries and the incisors, which is seen in *Steneofiber fossor* and the recent beavers. In this respect *Euhapsis platyceps* is more nearly like *Arctomys monax*, which has a continuous, almost horizontal palatal surface from the posterior nares to the incisors. The posterior limit of the premaxillaries in *Euhapsis* is just back of the long, narrow incisive foramina; thence the suture ascends in an almost vertical line immediately in front of the preorbital foramina to the superior borders of the zygomatic processes, and across the face in a slight posterior obliquity to meet the posterior process of the nasals. The anterior narial opening appears to have a greater transverse than vertical diameter. The nasals are not present in the type.

The Mandible.

The angle and the posterior part of the mandible are broken off. The fragment shows that the horizontal ramus is rather short, which is in keeping with the short cranium. The symphysis is long and heavy, inferiorly it terminates in a downward projecting process, similar to that in *Steneofiber fossor* and the recent beavers. The alveolar border is nearly parallel with the long axis of the jaw. The base of the coronoid process is present and indicates an exceedingly outward pointing direction of this process, which naturally corresponds to the widely separated glenoid cavities in the skull. The angle, perhaps, had similar characters to that in *Aplodontia*.

Measurements.

Greatest length of skull	60	mm.
Greatest width of skull	58	"
Greatest width of occiput at mastoid processes	47	"
Greatest width of muzzle	14	"
Vertical thickness of skull including occipital condyle to top of sagittal crest	19	"
Vertical thickness of skull including tympanic bulla	22	"
Vertical thickness of muzzle, approximately	12	"
Length of muzzle from zygomatic process to anterior nares	15	"
Distance from incisor to p^4	18	"
Distance from and including p^4, to and including occipital condyle	39	"
Greatest width of occipital condyles	15	"
Greatest vertical thickness of condyles	4	"
Greatest antero-posterior diameter of incisor	4.5	"
Greatest lateral diameter of incisor	5	"

Mandible.

Total antero-posterior diameter of the three grinders	10.5	"
Total antero-posterior diameter of $p_{\overline{4}}$	5	"
Total transverse diameter of $p_{\overline{4}}$	4.5	"
Total antero-posterior diameter of $m_{\overline{1}}$	2.5	"
Total transverse diameter of $m_{\overline{1}}$	3.2	"
Total antero-posterior diameter of $m_{\overline{2}}$	2.5	"
Total transverse diameter of $m_{\overline{2}}$	3.2	"
Depth of jaw at $p_{\overline{4}}$, including process on the chin	16	"
Depth of jaw at base of process on the chin	12.5	"
Depth of jaw at $m_{\overline{2}}$	10	"
Antero-posterior diameter from $p_{\overline{4}}$ to incisor (approximately)	11	"
Greatest length of the jaw-fragment	27	"

SUGGESTIONS REGARDING THE PROBABLE ORIGIN OF DÆMONELIX.

In 1891, Professor Erwin H. Barbour of the University of Nebraska discovered some peculiar fossils, called by him *Dæmonelix*.[1] After extensive study, he arrived at the conclusion that these strange forms were the remains of gigantic plants. Professor Cope[2] and Dr. Theodor Fuchs[3] suggested that the "explanation of these objects seems to be that they are the casts of the burrows of some large rodent." Mr. Joseph T. James,[4] in a paper read before the Biological Society of Washington, is inclined to associate *Dæmonelix* with certain small spiral concretions found in late Tertiary deposits in Switzerland, called "Screw-stones" by Oswald Heer.[5] These and *Dæmonelix*, James regards as belonging to the same order as *Spirophyton* (or *Taonurus*),[6] and *Spiraxis*[7] from the Chemung rocks of New York. He seems to hold the opinion that Heer was wrong in interpreting these screw-stones as casts of spiral tubes made by burrowing shells. The fact, however, that a specimen of a burrowing shell (*Lutraria senna*) was found in one of these spirals, carries more conviction with regard to the origin of them than mere speculation could do.

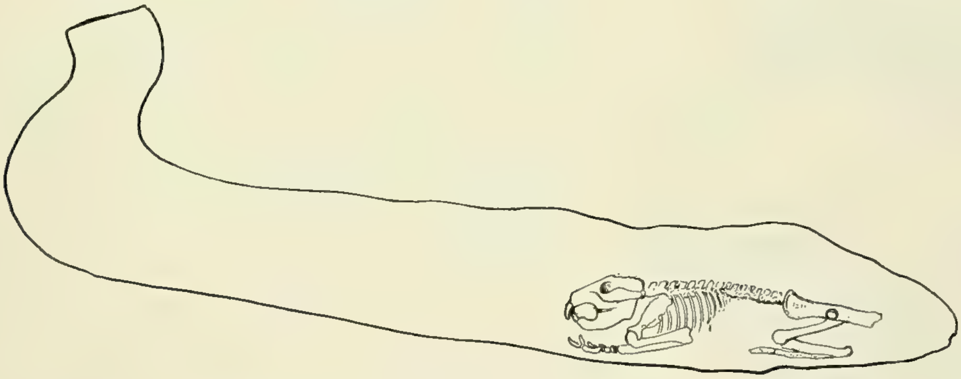


FIG. 5. Field sketch of a weathered rhizome containing the type-specimen of *Steneofiber barbouri*. No. 1210.

The party sent by the Carnegie Museum to northwestern Nebraska, into the *Dæmonelix* region, in the summer of 1904, was fortunate in discovering rodent remains inside of these "cork-screws" (see note in *Science*, September 9, 1904, p. 344). Recalling Professor Barbour's statement of having found remains of a rodent in a "rhizome" of *Dæmonelix*,[1] the search was vigorously carried on during our stay in this region.

---

[1] Notice of new gigantic fossils. *Science*, V., 19, pp. 99–100, and "Notes on a New Order of Gigantic Fossils," University Studies, No. 4, July, 1892, pp. 301–335, pl. 6.

[2] The *American Naturalist*, June, 1893, pp. 559–560.

[3] "Ueber die Natur von Dæmonelix Barbour," *Ann. k. k. Naturhist. Hofmus.*, Wien., 1893, pp. 91–94.

[4] *The American Geologist*, Vol. 15, No. 6, June, 1895, pp. 337–342.

[5] "Die Urwelt der Schweiz," 1865, p. 438.

[6] 16th Ann. Rep. Reg. Univ. New York, Albany, 1863, pp. 76–83.

[7] *Ann. N. Y. Ac. Sci.*, 3, 1885, pp. 217–220.

In a locality, where *Dæmonelix* is found in great numbers, one is always sure to find rodent (*Steneofiber*) remains. Considerable pains was taken to study these so called plants from all possible points of view, and the conclusions arrived at are at variance with those of the advocates of the plant-theory.

It seems reasonable to believe that *Dæmonelix* is the cast of a rodent-burrow for the following reasons. Remains of rodents, which possess highly developed fossorial characters are found inside of the casts. These rodents are of the proper size in comparison with the average size of *Dæmonelix.* I have seen no very small specimens of the latter exhibiting the wonderful regularity of form met with in the larger ones: such small ones as I have seen cannot properly be classified with the typical *Dæmonelix.*

On the hypothesis that these screws are casts of burrows, it would seem likely that in making them the rodents tamped and firmly packed the walls of their tunnels. The secretions of the animal, and the constant passing back and forth would, I think, greatly help to solidify the walls, since these habitations might have been occupied for a considerable length of time. In support of this it may be said that it is seldom that articulated skeletons are found in *Dæmonelix*, but in the majority of cases the bones are scattered (perhaps by the inhabitants of the burrow), and quite often only the head is found crowded close to the wall, or inside of the rim

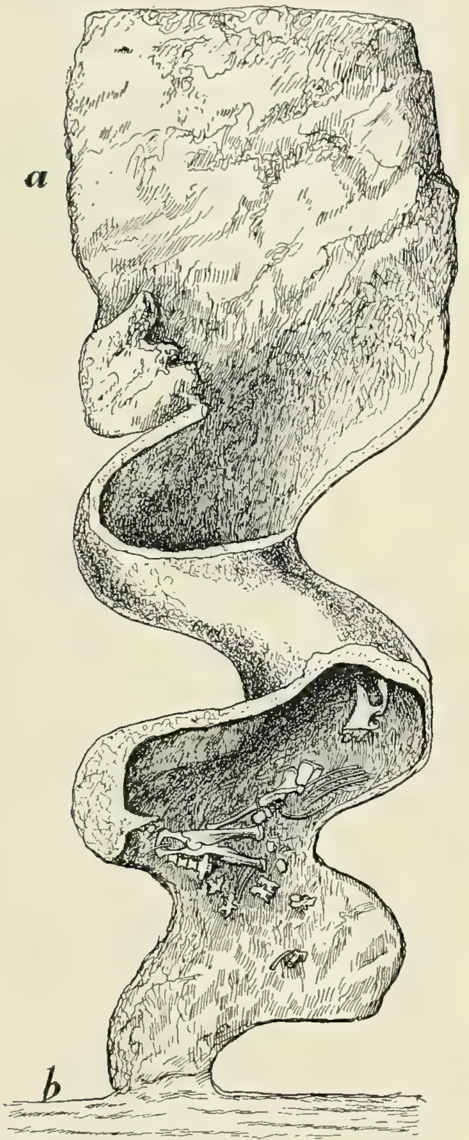


Fig. 6. A weathered portion of a *Dæmonelix* containing a skeleton of *Steneofiber fossor.* Total length of specimen from horizontal stratum *a* to *b*, approximately 61 cm.

---

[1] In passing through Lincoln, Nebraska, on my way East, I saw Professor Barbour who was kind enough to show me most of the *Dæmonelix* material in the museum. The rodent mentioned by him is about the right size to have made the mold of the specimen in which it was found. It is a *Steneofiber.*

of the compact mass of roots, which are to be spoken of later. In two cases skulls were found near the rounded ends of "rhizomes," and crowded close to the inside surface of the surrounding silicified zone of roots. The type-specimen of *Steneofiber fossor* (described in the preceding pages) was also found near the end of one of those "rhizomes."

The accompanying figure (Fig. 6) is a diagrammatic illustration intended to represent an actual specimen of an apparently incomplete *Dæmonelix* in the Carnegie Museum collections. This specimen was found by the writer, and presents some interesting features. It is a very short spiral, much weathered, and contains part of the skeleton of *Steneofiber fossor.* This short spiral was found, in situ, between two layers of more coherent material than that in which it was imbedded. The thin stratum below the lower end of the spiral (Fig. 6, *b*) is a horizontal layer of organic structure, some three or four inches thick, and intermixed with sand. This organic structure resembles some sheets of vegetable growth covered by a sudden influxes of sand brought in by water, and was simply a portion of the deposit in which the burrow was afterward made. The stratum overlying this specimen (Fig. 6, *a*) is also quite horizontal, but consists of much harder, silicified material, and is more irregular in thickness. Such hard layers of sandstones are quite common in these beds. The upper end of this specimen of *Dæmonelix* gradually loses its character, and cannot be traced upward into this hard cap of sandstone. The latter was probably formed by the deposition of sand in a pool of water on the surface of the ground. The exit of the *Dæmonelix* hole naturally lost its shape under these conditions.

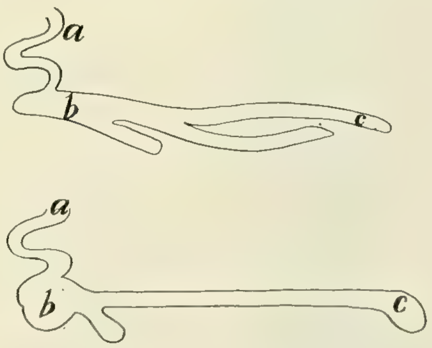


FIG. 7. Forms of *Dæmonelix* sometimes found. Taken from field sketch of exposed specimens lying on the surface with only the base of the vertical spiral attached to the "rhizome." *a* to *b*, 18 inches; *b* to *c*, 14 feet.

The more perfect specimens of *Dæmonelix* possess so-called "rhizomes," which are nearly always larger in circumference than the vertical spiral. Occasionally, this "rootstalk" is branched, two, three, and even more times. Each of the branches is of approximately the same general size, with local enlargements and pockets up to the extreme blunt and rounded end. No instance was found of these "rhizomes" crossing one another, so as to form a short kink, such as is often seen in roots of recent plants. The end of the rhizomes is often found enlarged in a more or less hemispherical manner. I have often traced them for six, and sometimes for fifteen feet from the base of the spiral to their end.

The most perfect specimens of *Dæmonelix* have an average diameter of about 6 to 10 inches. Quite often large specimens are found, that have not the even symmetry of the spiral. Again there were others representing, perhaps, burrows made by an entirely different animal, large enough at the surface to admit parts of a skeleton of a larger mammal, such as Professor Barbour discovered in an irregular fragment of *Dæmonelix.* Such, however, might also be burrows that have caved in causing the entombment of larger objects partially within the burrows.

A few small colonies of Prairie Dogs (*Cynomys ludovicianus*) are found on the table land between the Niobrara River and the northern exposure of the Miocene formation ("Pine Ridge"). Our party (consisting of Messrs. T. F. Olcott, A. A. Dodd, and the writer) had become so interested in the study of *Dæmonelix,* that it was decided to make a few experiments in digging out the burrows of these recent fossorial animals. A quantity of plaster of paris was accordingly purchased, and with a large mortar box, a barrel of water, and a supply of sand we set out for the prairie dog town, to make some casts of these burrows. The accompanying diagrams (Figs. 9 and 10) show that we were partially successful, if not in finding a symmetrical spiral, at least in getting casts that were irregular like some specimens of *Dæmonelix* (see Barbour's illustrations, figs. 17, 18, and 19 in Bull. Geol. Soc. Amer., Vol. 8, 1897, pp. 305–314). There were found, in the casts of these burrows, many fine rootlets at a depth of 4 or 5 feet below the surface. The nest (Fig. 9, *d*) was well bedded with dry grass brought down from the surface. Mixed with this bedding were many beetle-wings, worms, and remains of grasshoppers. Particular attention was paid to the solidity of the burrows. It is remarkable how firm the walls of these tunnels are in this loose and rather incoherent sand, which is a redeposition of the eroded Miocene sediment.

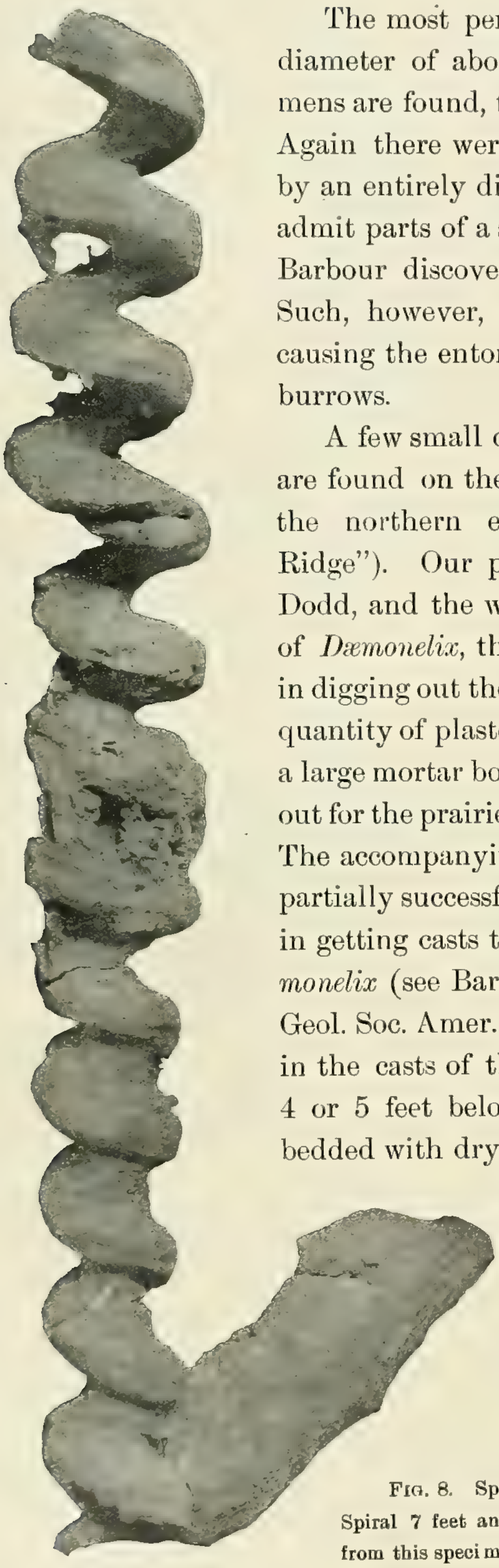


FIG. 8. Spiral and part of "rhizome" of *Dæmonelix*, No. 17 (field number). Spiral 7 feet and 8 in. long. Many microscopic slides (Pl. XXI.) were taken from this specimen.

It seems reasonable, that, after our Miocene rodents vacated their burrows, the roots of plants growing on the surface would find their way down the spirals as well as down the straight shafts. The tamped walls remained harder than the surrounding ground, and when the roots and rootlets reached these walls, they followed the line of contact between the walls and the inside filling, perhaps similar to the roots of a potted plant. Occasionally a root would pierce the wall, and continue on its way to the next coil. This is seen on nearly all specimens of *Dæmonelix.* As has been stated before, there is a cylinder of tangled roots on the outside surface of *Dæmonelix.* Toward the center of the casts the roots are much less numerous.

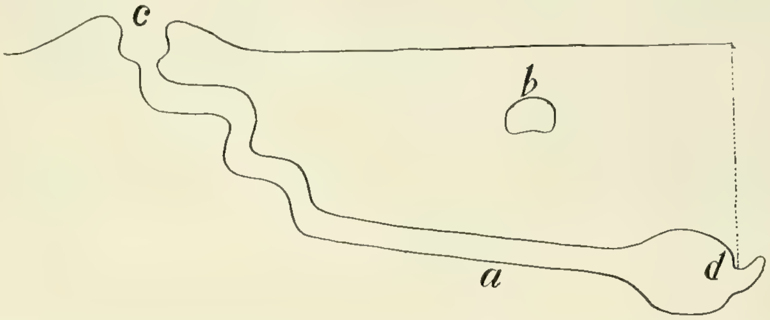


Fig. 9. A newly dug prairie dog burrow. From a field diagram. *c*, Exit of burrow ; *a*, nearly horizontal tunnel about 5 inches in diameter ; *d*, nest 8 inches in diameter and four feet under surface ; *b*, cross-section near nest showing emargination of cast caused by bedding. From *c* to *d*, 9 feet.

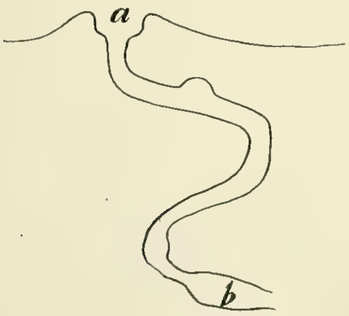


Fig. 10.

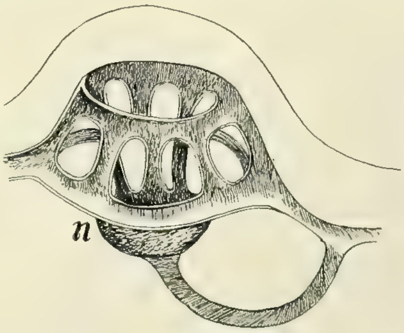


Fig. 11.

Fig. 10. Diagram of cast of an old burrow of Prairie Dog. *a*, exit ; *b*, at this place the burrow was caved in. From *a* to *b*, 10 feet.

Fig. 11. An underground fortress of a mole, *Talpa europæa ;* after J. G. Woods, in "Homes Without Hands." *n*, nest.

In speaking of the recent mole, J. G. Woods (in "Homes Without Hands") says that "we do not generally know the extent or variety of this animal's tunnels or that it works on a regular system, and does not burrow here and there at random." In this volume is an illustration of a mole-hill (Fig. 11), which is represented (by permission of the publisher) in the accompanying figure. If this illustration correctly represents the actual habitation of the animal, it must at once be admitted that *Steneofiber*, which I think is responsible for *Dæmonelix*, has an able competitor in underground engineering in our recent mole.

It cannot be denied that certain features of *Dæmonelix*, for instance the straight vertical axis inside of the spiral, are not easily explained, and that we have not yet arrived at a complete understanding of all the details connected with these structures; but it is very likely that these difficulties will be removed, when we know more of the underground habitations of fossorial animals.

The following notes are observations by Mr. O. E. Jennings, custodian in the Department of Botany, kindly submitted to the writer for publication in connection with this paper.

NOTES ON THE VEGETABLE TISSUES IN DÆMONELIX.

An examination of thirty-two microscopical sections obtained from various parts of the so-called devil's corkscrews (*Dæmonelix*), in the collections of the Carnegie Museum, invariably revealed the fossilized remains of vegetable tissue. Although the sections had been cut from many different places in the *Dæmonelix* specimens, the vegetable tissues were usually more abundant in those sections obtained near the surface of the specimens, and the tissues in these sections gave better results under the microscope. The sections best showing the cellular structure and the differentiation of tissues were longitudinal sections cut parallel to the surface of the so-called corkscrews. A careful study of the slides involved the examination of a large number of tissue fragments, as in some of the slides, at least one fourth of the total area of the section was occupied by plant remains.

The vegetable tissues are apparently simply the remains of a mesh of roots such as is sometimes found clogging a tile drain or sewer. The tissues were most commonly found in the form of hollow tubes, such as would be obtained by sectioning rubber tubing at various angles. The central portion of the root has, in most cases, disappeared leaving only the outer tissues — the epidermis and the cortex. The root cap was searched for in vain, although root-hairs were rather common.

The reason, that the thin epidermal covering and the rather large thin-walled cells of the cortical tissue should be the best preserved, may be, that these parts of a living root soon become more or less impervious to water. That portion of a living root just back of the tip is the most absorptive. In the older portions farther back the epidermis may have become cutinized, or the cortex may have become suberized, or both; in either event the tissue thus becomes impervious to both water and gases.

On the other hand, the tissues of the central portion of the root, the stele, even though they may have become lignified or woody, are still permeable to these fluids, and thus can be readily entered by some of the bacteria of decomposition.

A few sections were found showing more or less completely the entire structure of the root, but the detail of the vascular bundle could be made out only with considerable difficulty, as the cells were usually very dark and the structure mostly obliterated. Enough was evident, however, to plainly indicate that nearly all of the roots were those of angiosperms, the cells discerned being quite typical. Rather large tracheæ, with the customary rings and reticulations, together with longer cells of a smaller diameter, some of the latter also showing reticulations, were quite plainly to be seen in the stele. No pith cells were evident but the woody elements were enclosed by a well developed bundle sheath. Fragments of older roots with a strongly developed cortical region were found; in some of these the rectangular cortical cells were built up with all the regularity of brickwork, each successive layer being regularly and perpendicularly superimposed.

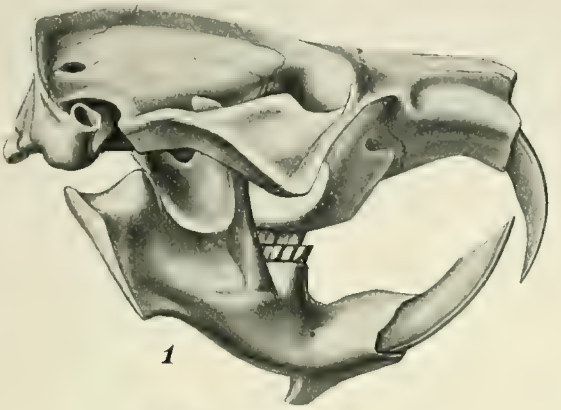
One of the main structural differences between stems and roots lies in the manner in which branches originate. In stems the branches originate near the surface but in roots the branches originate on the vascular cylinder and burrow upward through the cortex thus disturbing the arrangement of the cortical cells. An example of this was found in one of the sections, as may be seen by consulting the figure.

Carnegie Museum, January 24, 1905.

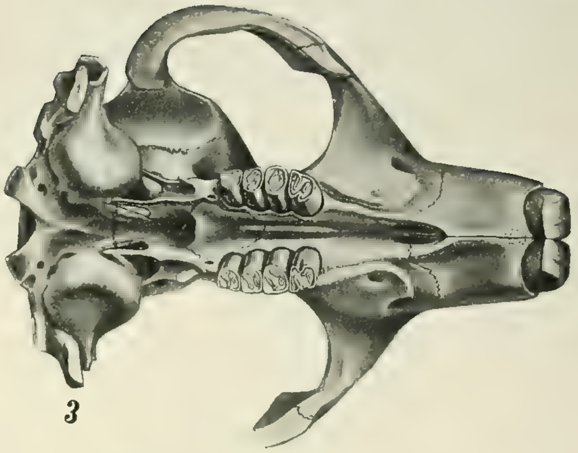
EXPLANATION OF PLATE XVII.

Fig. 1. *Steneofiber fossor*, type No. 1217. Side view of skull and lower jaws.
Fig. 2. *Steneofiber fossor*, type No. 1217. Top view of skull.
Fig. 3. *Steneofiber fossor*, cotype, No. 1208. Palate view of skull.
Fig. 4. *Steneofiber fossor*, cotype, No. 1208. Crown view of inferior dentition.
Fig. 5. *Euhapsis platyceps*, type No. 1220. Side view of skull.
Fig. 6. *Euhapsis platyceps*. Palate view of skull.
Fig. 7. *Euhapsis platyceps*. Top view of skull.
Fig. 8. *Euhapsis platyceps*. Crown view of inferior dentition.
Fig. 9. *Steneofiber barbouri*, type No. 1210. Palate view of skull.

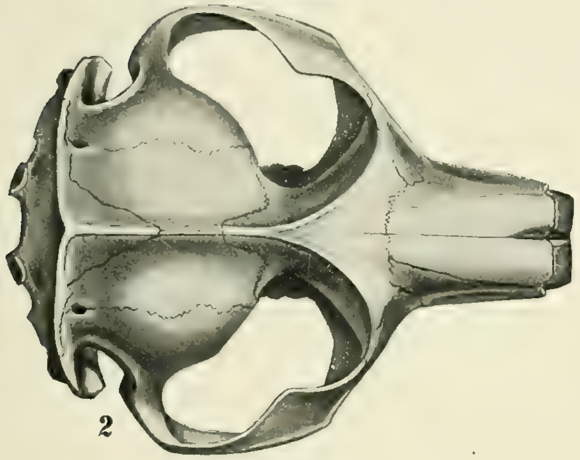
All figures natural size.



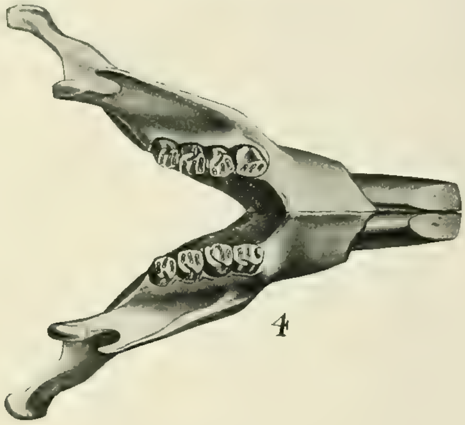
1



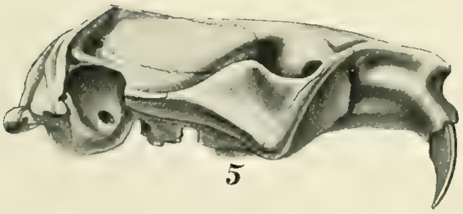
3



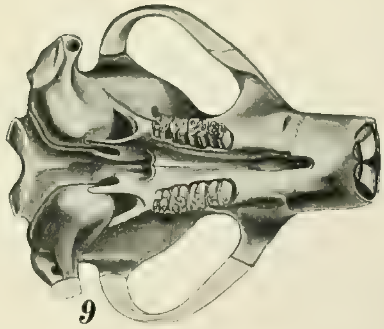
2



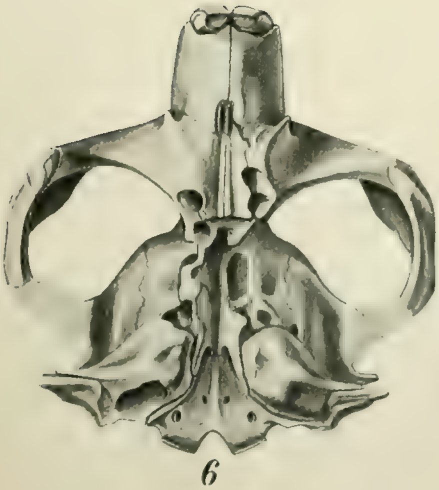
4



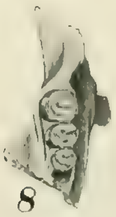
5



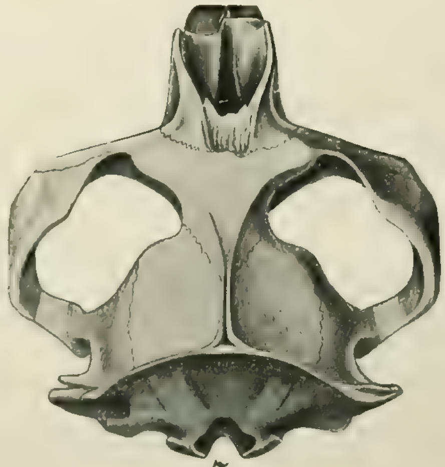
9



6



8



7

Sydney Prentice, del.

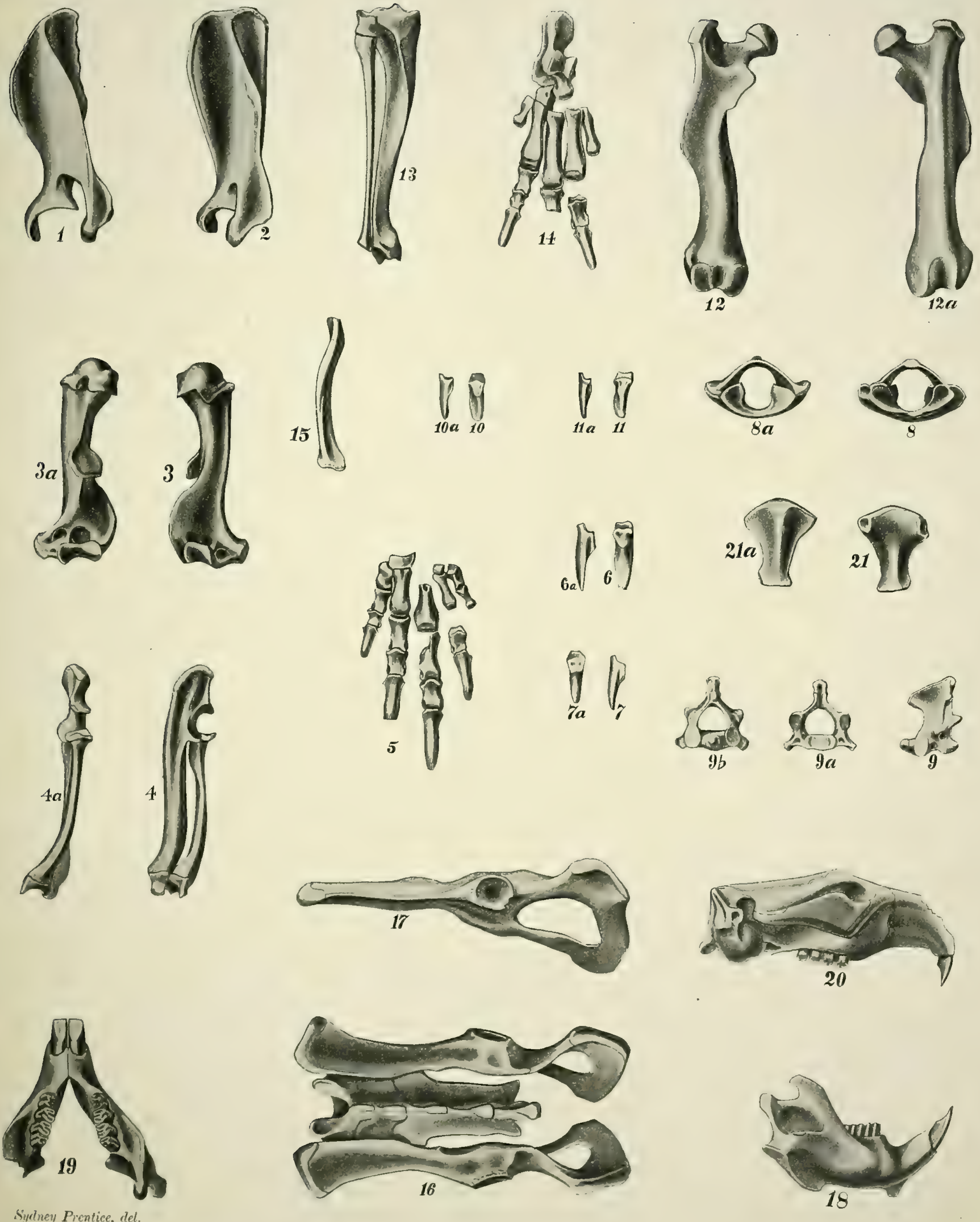
Fossil Rodents from the Upper Miocene, Harrison Beds. All Figures Natural Size.

EXPLANATION OF PLATE XVIII.

FIG. 1. *S. fossor*, type. External view of scapula.
FIG. 2. *S. fossor*, cotype. External view of scapula.
FIG. 3. *S. fossor*, type. Posterior view of humerus.
FIG. 3*a*. *S. fossor*, type. Anterior view of humerus.
FIG. 4. *S. fossor*, type. Internal view of radius and ulna.
FIG. 4*a*. *S. fossor*, type. Anterior view of radius and ulna.
FIG. 5. *S. fossor*. Dorsal view of manus. Composite.
FIG. 6. *S. fossor*. Plantar view of ungual phalanx, third digit of manus.
FIG. 6*a*. Side view of same phalanx.
FIG. 7. *S. fossor*. Side view of phalanx, second digit of manus.
FIG. 7*a*. Plantar view of same bone.
FIG. 8. *S. fossor*, type. Posterior view of atlas.
FIG. 8*a*. *S. fossor*, type. Anterior view of atlas.
FIG. 9. *S. fossor*, cotype. Side view of axis and third cervical showing coössification.
FIG. 9*a*. *S. fossor*, cotype. Posterior view of axis.
FIG. 9*b*. Anterior view of same bone.
FIG. 10. *S. fossor*, type. Plantar view of ungual phalanx, fourth digit of pes.
FIG. 10*a*. Side view of same bone.
FIG. 11. *S. fossor*, type. Plantar view of ungual phalanx of pes.
FIG. 11*a*. Side view of same bone.
FIG. 12. *S. fossor*, type. Posterior view of left femur.
FIG. 12*a*. Anterior view of same.
FIG. 13. *S. fossor*, type. Anterior view of tibia and fibula.
FIG. 14. *S. fossor*, type. Dorsal view of pes.
FIG. 15. *S. fossor*, cotype. An oblique view of right clavicle.
FIG. 16. *S. fossor*, type. Superior view of pelvis.
FIG. 17. *S. fossor*, type. View of left side of pelvis.
FIG. 18. *S. barbouri*, type. Side view of right mandible.
FIG. 19. *S. barbouri*, type. Crown view of inferior dentition.
FIG. 20. *S. barbouri*, type. Side view of skull.
FIG. 21. *S. fossor*, cotype. Superior view of presternum.
FIG. 21*a*. *S. fossor*, cotype. Inferior view of presternum.

All figures natural size.

Plate XVIII.



Sydney Prentice, del.

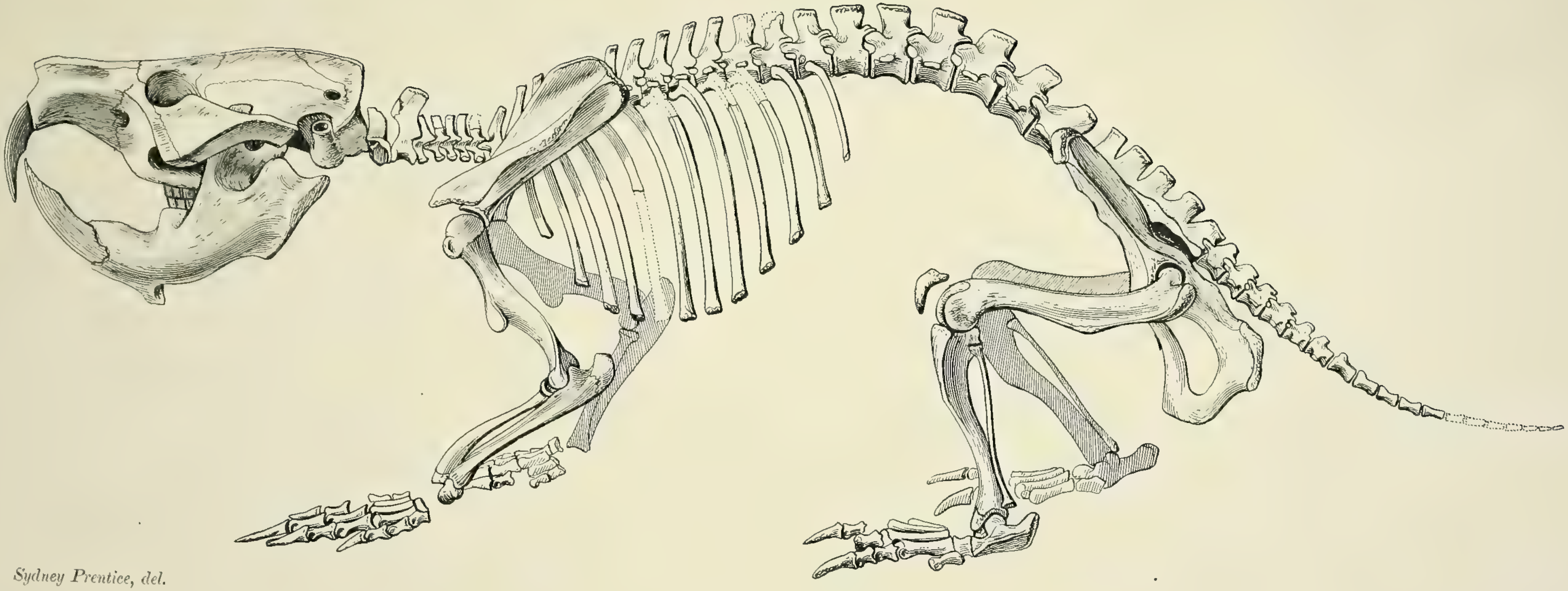
Fossil Rodents from the Upper Miocene, Harrison Beds. All Figures Natural Size.

EXPLANATION OF PLATE XIX.

S. fossor, type 1217. Restoration of the skeleton.

The scapula is drawn from the cotype No. 1208 and the greater part of the fore-foot from specimen No. 1204.

The figure is approximately $\frac{3}{4}$ natural size.

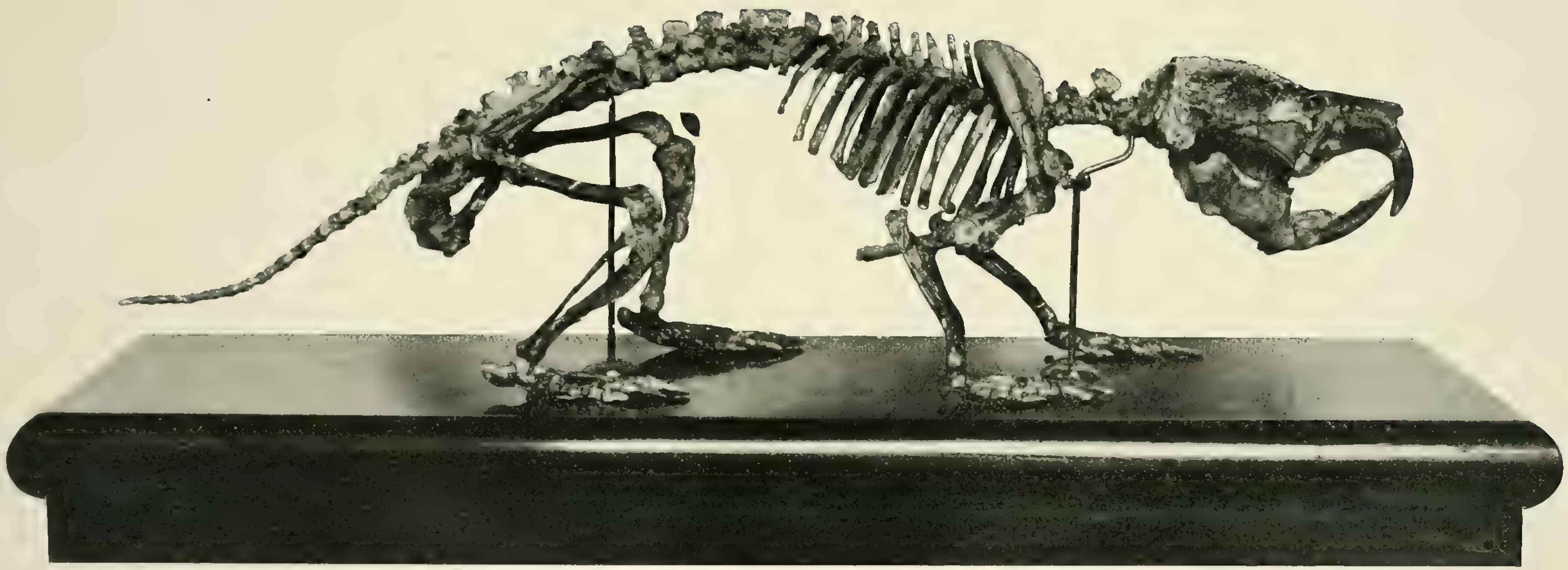


Sydney Prentice, del.

RESTORATION OF *STENEOFIBER FOSSOR.* $\frac{3}{4}$ NATURAL SIZE.

EXPLANATION OF PLATE XX.

Steneofiber fossor, type 1217. Mounted skeleton $\frac{4}{7}$ natural size. The greater part of the right fore-foot is from specimen No. 1204. Part of the sternum, the superior part of the left scapula, the left fore-foot, the greater part of the left hind-foot, and the tip of the tail, are reproduced in plaster of paris.



MOUNTED SKELETON OF *STENEOFIBER FOSSOR*. ABOUT $\frac{4}{7}$ NATURAL SIZE.

EXPLANATION OF PLATE XXI.

Fig. 1*a*. Section from *Dæmonelix* showing fossilized root remains. Two small rootlets with root-hairs, *h*, grew into the cavity formed by the decomposition of a larger root. *r*, bundle sheath enclosing the outer portion of the vascular bundle. × 65. (Eighth ring from bottom, *Dæmonelix* 17. Harrison Beds, Sioux Co., Nebraska.)

Fig. 1*b*. Cross-section of rootlet as usually found in *Dæmonelix*. Only the epidermal and cortical tissues are preserved. × 65. (Transverse section of *Dæmonelix* cake (late Miocene). Upper Monroe Creek Beds, Sioux Co., Neb.)

Fig. 2. Longitudinal section of rootlet showing epidermal tissue and, *h*, root-hairs. × 65. (Section from Ring 4, *Dæmonelix* 17. Taken close to the surface of specimen.)

Fig. 3. Cross-section of rootlet showing the stele or vascular bundle, *s*, and sand grains, *p*. × 65. (From the interior of Ring 8, *Dæmonelix* 17.)

Fig. 4. Cross-section of central portion of root showing the bundle sheath, *c*, with vascular tissue inside and cortical tissue outside. × 65. (Ring 12, *Dæmonelix* 17.)

Fig. 5. Longitudinal section of root showing the method of branching. × 31. *s*, stele. (Longisection of *Dæmonelix* "cake" from near its edge (late Miocene), Upper Monroe Creek Beds, Sioux Co., Neb.)

Fig. 6. Section taken longitudinally and including a bend in the root. *s*, stele. × 50. (Section taken parallel to the surface of "rhizome" of *Dæmonelix* 17. Harrison Beds, Sioux Co., Neb.)

Fig. 7. Portion of same showing part of the stele at a greater magnification. *w*, tracheary vessels or wood cells. × 275.

Fig. 8. Portion of same stele still more enlarged. *c*, cortical cells; *b*, bundle sheath; *x*, reticulated wood vessel. × 400.

Fig. 9. Section from fragment of an older root showing a regular superimposition of the cortical cells, *c*. × 65.

Fig. 10. Cross-section in same fragment showing, *w*, woody tissue and, *c*, cortex. × 65.

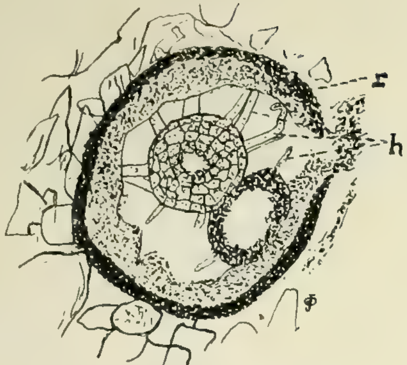


Fig. 1a.

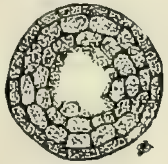


Fig. 1b.

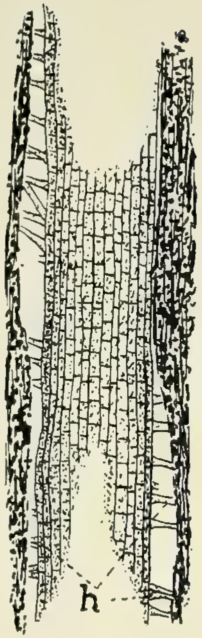


Fig. 2.

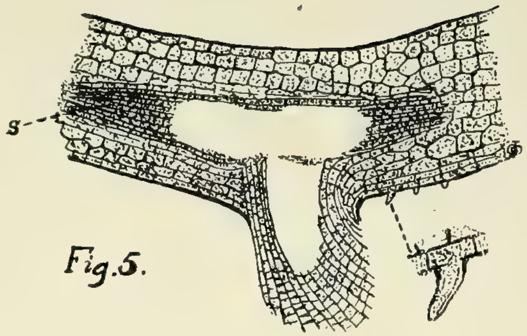


Fig. 5.

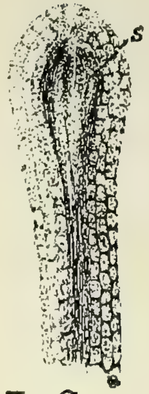


Fig. 6.

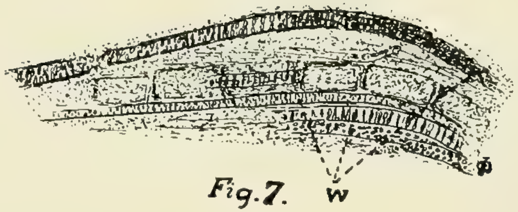


Fig. 7.

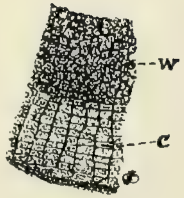


Fig. 10.

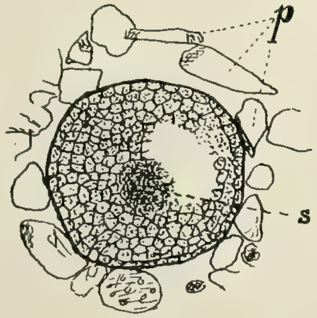


Fig. 3.

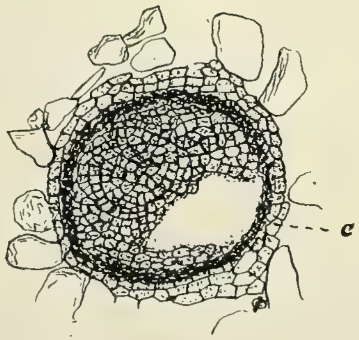


Fig. 4.

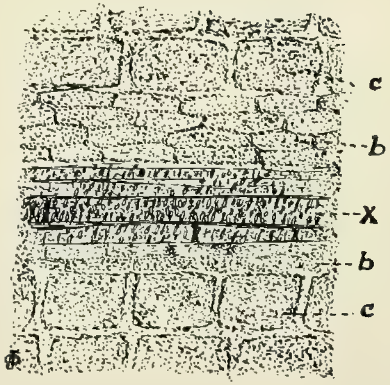


Fig. 8.

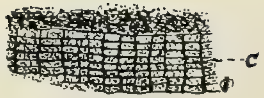


Fig. 9.

O. E. Jennings, del.

MICROSCOPIC SECTIONS OF CELLULAR STRUCTURES IN *DÆMONELIX*. GREATLY MAGNIFIED.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 5.

THE TERTIARY OF MONTANA.

BY EARL DOUGLASS.

INTRODUCTORY REMARKS.

It has long been the wish of the writer, to prepare a memoir, complete as it is possible to make it, on the Tertiary formations of western Montana, the object being a restoration, so far as is practicable, of Tertiary times there, to accumulate data so that fairly accurate mental pictures of the conditions at the different periods may be obtained. It is not only interesting to thoroughly study the extinct mammals, which are the most abundant fossils, but to ascertain, as far as possible, what other animals lived at the same time, what plants flourished, and what were the physical conditions generally. Was it a land of mountain chains with intervening valleys as it is now, or was it a vast plain with the late Cretaceous mountains worn nearly down to the sea level? Was the climate dry and the land a dusty, windy waste, or was it a region of lowland forests, rich green uplands, great lakes and broad rivers? Was it a time of upheaval of the strata, of earthquakes, and of volcanic eruptions, that made streams of molten rock, charged the waters with debris, and made the sky gloomy with floating dust; or did each of these conditions prevail at some time during this long period? Was the climate mild and uniform, or were there cold winter storms; and was the land hidden in snow, and the waters imprisoned in ice, during a part of the year? What can we learn concerning the strange creatures of the times, whence they came, and whither they went? Were the forests, if there were any, the same as those we find there now, or have they, with the animals, changed? Can we throw any light on the past migration of plants and animals? What do these few fragmentary chapters teach us with regard to the transmutation of animal life?

These are all interesting questions, and we feel sure that by patient, careful study we may approach nearer and nearer the solution. In the inquiry we need an imagination broad enough to encompass all the possibilities; but the conclusions must be based on evidence alone. We must carefully avoid the accumulation of a chaos of facts on the one hand, and a glittering but frail structure of theories on the other. These problems furnish an ideal toward which to work. There are data bearing on nearly all; yet it is not expected that all can be completely solved here. It will require all the data available and all the talent of all the men working in this field of investigation to even approximately solve them; yet it is felt by the writer that certain aspects of the problems can be better seen by becoming more familiar with a certain area the boundaries of which are more or less definite, and where so many different horizons, with their several faunas, are represented.

The work done by the writer in this region has been primarily that of collecting, and there has not been time for an accurate survey of the extensive field; yet a large number of observations have been made, and many data have been collected from other sources bearing on the solutions of the problems here involved. As the data have accumulated, conceptions apparently more and more in harmony with the facts have gradually taken the place of ideas at first entertained.

It was originally intended to prepare the material and embody it in one comprehensive memoir, but this requires years of work, and it would too long defer the publication of interesting discoveries and results. It has been thought best, therefore, to issue it in parts uniform in style, so that if required, the parts can be bound together in one complete volume, after all have been issued.

To Dr. Wm. J. Holland, the Director of the Museum, and, since the death of Mr. J. B. Hatcher, the acting Curator of Vertebrate Paleontology, I am indebted for the free and unrestricted use of the material. The Montana fossils were collected by myself, or by expeditions in my charge. The drawings for this issue were made by Mr. Sydney Prentice, the draftsman for the Carnegie Museum.

PART I. A NEW MONOTREME-LIKE MAMMAL.

Xenotherium unicum gen. and sp. nov.

(Plate XXII., Figs. 13, 14, 15 and 16.)

One of the most interesting specimens from the Titanotherium Beds at McCarty's Mountain is a nearly perfect skull, which is unlike that of any Eutherian mammal with which I am acquainted; but in most of its characters is very much like the living Monotremes of the Australian region. The only essential skull characters which distinguish it from modern Monotremes are (*a*) the possession of tympanic bullæ, and (*b*) distinct alveoli for cheek teeth, which appear to have been simple, one rooted, peg-shaped, and six in number on each side.

Among the fossils found near the same level were *Helodermoides, Ictops major, Ischyromys, Hyænodon, Agriochœrus, Limnenetes, Hyracodon,* and *Titanotherium.*

PRINCIPAL CHARACTERS.

Characters of skull.—All the bones of the skull united into one piece, and the sutures, for the most part, obliterated; cranium short with nearly the form of a pear divided in half longitudinally, large and full in the occipital region, tapering rapidly forward to the rather short, low muzzle, broad and slightly convex on top; a large portion of the brain case behind the vertical lambdoid ridges; supraorbital ridges far apart and but faintly discernible; no post-orbital processes on the temporals; zygomatic arches complete, but slender; two infraorbital foramina; foramen magnum large with an extension upward in the occipital; tympanic bullæ present and well developed; pterygoids tending to arch over the space between the posterior portion of the palate, and the tympanic bullæ, but the arch not completed; premaxillaries extending beyond the anterior border of the palate, first diverging and then tending to converge again above.

There are on each side only six alveoli for teeth. These are arranged in longitudinal rows, and there were apparently only six simple, one-rooted teeth on each side. Only the last tooth is preserved and that is a minute peg, scarcely projecting below the palate but apparently covered with enamel. The lower surface is polished and slightly worn by attrition. The anterior tooth was much the largest, and its root evidently extended backward toward the orbit.

MEASUREMENTS.

Length of skull	3.3 cm.
Width of skull at lambdoid ridges	2.3 "
Height of skull	1.33 "
Length of dental series	.9 "

DETAILED DESCRIPTION.

Dentition.—There were apparently six teeth on each side of the upper jaw. The anterior alveolus by its size and the backward extension above and outside of the other teeth shows that this contained a one-rooted caniniform tooth. The posterior alveolus is small and still contains one minute, simple, peg-shaped tooth on each side. The other alveoli appear to have each held a one-rooted tooth. On one side the premaxillary is nearly complete and the one on the other side is less so. On these anterior projections of the maxillaries there is no vestige, or suggestion of incisors, but on the anterior portion of the palate, it looks as though there might have been rudimentary teeth earlier in life.

The anterior alveolus is the largest, is nearly circular, and appears to have held a canine tooth. It extends backward and outward toward the orbit. Its position is indicated by a curved ridge on the maxillary. The second and third alveoli are nearly equal in size; but the fourth, fifth, and sixth diminish in size posteriorly, the last containing a minute tooth. The second, third, and fourth alveoli appear to be antero-internally and postero-externally oblique; and it appears on the outside of the maxillary that the roots of the second and third extend obliquely backward in the same direction as the supposed canine.

The last two teeth—one on each side—are the only ones preserved. They are small, simple, and cylindrical, with only a small blunt point projecting a trifle below the border of the alveolus and the palate. They appear to be covered with enamel as they are black and shiny. The lower surface of one is convex and roughened, with shallow pits and ridges, but I cannot make out any definite pattern. The other tooth is slightly worn or polished on the edge.

The Skull.

The bones of the skull are so thoroughly cemented together that it is difficult or impossible to make out many of the sutures. The muzzle is low and short, and at the canine alveolus twice as wide as high. The portion occupied by the nasals is convex. A curved convexity extends backward from the alveolus of the canine to near the orbits. If the portions anterior to the supposed canine are premaxillaries, then these bones unite below forming the anterior portion of the palate. The processes are separate above and diverge; but anteriorly there is a tendency, as in living Monotremes, to converge. Part of the anterior portions of the nasals are missing. The lines that appear to show the former position of the nasal and nasomaxillary sutures are fairly plain. The nasals are quite long and narrow, and are uniform in width as far as shown. The anterior border of the palate is slightly thickened, and an obscure lobing, with a suggestion of foramina, may indicate the former presence of rudimentary or deciduous incisors. The top of the skull is broad and nearly flat, yet somewhat convex antero-posteriorly and transversely. The most prominent portion (the greatest convexity) is near the middle of the upper surface of the cranium a little farther back than the orbits. The supra-temporal ridges are represented by faint (yet quite readily traceable) lines extending from the anterior portion of the orbito-temporal fossa upward, backward, and toward the middle line of the skull, then turning outward, making a quite regular curve, and ending at the peculiar lambdoid ridges on the roof of the cranium. These faint supratemporal ridges never come near each other, so there is no sagittal crest; yet there is a faint line, or narrow longitudinal ridge, on the middle line of the skull. The post-orbital constriction is extremely slight as seen from above; but is more noticeable inside the orbito-temporal fossa. The former position of what were probably the fronto-parietal sutures may be faintly distinguished. Faint lines extend in a transverse direction on the skull at the post-orbital constriction, but near the middle line they turn backward and meet, thus forming a V-shaped figure.

The lambdoid ridges are continuous with the posterior portion of the zygoma. Just back of the auditory meatus they curve upward and ascend the brain-case vertically. Toward the top of the brain-case they trend slightly backward, and more so as they approach and meet each other at the upper portion of the occiput. These ridges are quite prominent on the sides, but become minute, low and narrow, on top. Here the skull is highest and widest.

The Occipital Region. — This region may be said to be divided into three lobes or convexities — a median inferior one, and two large lateral ones. The lateral ones are separated above by a thread-like median ridge continuous with the lambdoid ridges, and their lower portion by the median convexity. From the latter, they are separated by a shallow depression or concavity. The foramen magnum is large. The opening extends upward above the occipital condyles.

The occipital condyles are broad, and far apart above. The surfaces for the articulation with the atlas nearly meet below. Above each condyle is a small concavity. The basioccipital is partly hidden by the auditory bullæ, which are large and coössified with the exoccipitals, squamosals and pterygoids. They are somewhat flattened vertically — that is, they are not so nearly spherical as in some other mammals; though they are considerably inflated as seen from below. They are broadest internally, and narrow toward the external auditory meatus, which is short. They are three sided; two of the sides are convex; the anterior one is concave. There is a convexity on the middle of the lower surface and one on the inner border extending from the pterygoid backward nearly to the occipital condyle. The pterygoids partly arch over the space behind the posterior nares, but leave a slit between them, which is widest in front. This may, perhaps, be considered as a tendency toward a character seen in modern Monotremes, the moving backward of the posterior narial opening. The glenoid surface is comparatively large and flat, and is bounded posteriorly by the auditory bullæ. The palate is quite long and is longitudinally convex in the middle, with parallel convexities on each side between this and the alveoli.

RELATIONSHIP.

The general appearance of the skull is strikingly like that of the Monotremes. In fact, with the exception of the presence of tympanic bullæ and rooted teeth, it differs in no essential particular from *Ornithorhynchus* or *Echidna.* The presence or absence of tympanic bullæ has little significance in this connection, as it has been independently developed in so many widely different mammals. The Monotremes have a tympanic ring. In some cases this may have developed into a bulla.

The teeth differ from those found in *Ornithorhynchus* in being peg-shaped, and in being set in quite deep and well-defined alveoli. The number is also greater than in the latter genus, there being, apparently, six in each side of the jaw instead of two or three. In the new genus, too, there was one tooth which was caniniform. In *Ornithorhynchus,* the teeth, which are low-crowned, appear to have small roots.

But when we consider the vast dissimilarity in the different teeth of some individuals—for example, in certain Multituberculates, Insectivores, Marsupials, etc.—to say nothing of the astonishing differences and variety in the structure of the teeth in the subclass Eutheria, we could hardly exclude this animal from the Monotremata on these grounds. In fact, they appear quite insignificant. That the Monotremes have had a long history, and that they developed into a considerable diversity of forms is made evident by the marked minor differences of the two or three existing genera.

But since the idea of development has taken possession of biologists there has been a great temptation to see relationship where none exists. There is a vast interval, both in time and space, between early White River times in the Rocky Mountains and the Australian region of to-day, and we have but a single skull by which to judge. Yet if we were looking for a Monotreme in these older beds we could hardly expect it to be so much like that of the living species as is the fossil.

The general appearance of the skull is most like that of *Echidna;* though in a few details it more resembles *Ornithorhynchus.* If we could take a skull of *Echidna,* shorten its muzzle, give it tympanic bullæ and simple cylindrical teeth, make the orbito-temporal fossa like that of the duckbill, and premaxillaries similar to those of the latter, but much shorter, we would have a skull similar in all its principal characters to the fossil.

If this is the skull of a Monotreme it certainly is of great interest. If not, it is perhaps even more so; as, so far as I can learn, there is nothing like it among the Eutheria.

PART II. LEPTICTIDÆ OF THE LOWER WHITE RIVER BEDS.

Nearly sixty years ago, a man who resided at one of the posts of the St. Louis Fur Company, on the Missouri River, sent to Dr. Hiram Prout, of St. Louis, a fragment of the lower jaw of a large and unknown animal. It was found in the Bad Lands of White River, about sixty miles east of the Black Hills. Dr. Prout described and figured this jaw — the last molar of which was complete — in the American Journal of Science (1847). From the resemblance of the last lower molar to that of *Palæotherium* of the European Tertiary, it was supposed to belong to that genus. This is what is now known as *Titanotherium*, and it was the first mammalian fossil described from the White River Beds of the West. Since then all the parts of the skeleton and hundreds of skulls of this animal have been found, and all from the lower horizon of the White River. Besides this, skulls and skeletons of the large *Elotherium*, *Metamynodon*, *Trigonias*, and other Rhinoceroses have been obtained ; but aside from these, previous to the discoveries in Montana, almost nothing was known of the immediate precursors of the abundant and varied fauna, which had been so well preserved in the overlying Oreodon Beds.

In the year 1900 the present writer discovered, in three localities in Montana, remains of smaller mammals associated with *Titanotherium*. Of these about a dozen species were described.[1] The types were teeth, jaws, and portions of skulls. Among these, only one skull was nearly complete.

The American Museum Expedition to Western Montana in 1902, discovered nearly a dozen more species. These were all represented by jaw fragments with teeth. Twenty-three species and six new genera had now been described, principally from teeth and jaws. They were of much interest, as they represented a new fauna, and gave a better basis for comparison of the mammals of the Titanotherium Beds with those of the overlying Oreodon Beds. They were mostly small animals — marsupials, insectivores, rodents, and small ungulates.

In the summer of 1903, the Carnegie Museum Expedition in charge of the present writer, discovered a locality on the Bighole River, near McCarty's Mountain, north of Dillon, in Montana, which yielded far more complete specimens of this smaller fauna. In this collection there are many skulls of smaller animals — some almost complete — with portions of skeletons, also jaws with fuller teeth series, of larger animals.

These specimens, so far as they have been studied, do not appear to lessen the hiatus between the Titanotherium and Oreodon Beds, or the greater one between the former and the Uinta.

---

[1] *Trans. Am. Philos. Soc. N. S.*, Vol. XX., pp. 237–279. *Ann. Carnegie Mus.*, Vol. II., No. 2, pp. 145–150.

Among the fossils from the Titanotherium horizon in Montana are several specimens of *Ictops*. The best of these are from the beds near McCarty's Mountain, north of Dillon. Two species have been described by Dr. Matthew and myself from beds of the same age on Pipestone Creek in the vicinity of Whitehall. The latter were described from fragments of jaws with teeth. One imperfect skull was found near Three Forks associated with *Titanotherium*. From the deposits near McCarty's Mountain there are four specimens, all differing in size and in other particulars. All are represented by teeth, three by good parts of skulls, and two by skulls pretty nearly complete. Two were from near the same level; one was slightly, and another considerably, lower. There appear to be similar characters in the specimens from the Titanotherium Beds which distinguish them from those of the Oreodon Beds, yet the latter have not been prepared and thoroughly studied. We have in the Carnegie Museum some good portions of skulls from the Oreodon Beds of Sioux County, Nebraska; but they are either young, crushed, or injured in other ways, and are not in a condition for careful comparison. The specimens now under consideration are not distorted, and most of the teeth are beautifully preserved.

Though the specimens differ a good deal, they, perhaps, more resemble each other than they do the Leptictidæ of the Middle White River. Perhaps the most interesting thing about these little animals, at the present, is a study of their variations, and the light it throws, however little it may be, on the modes of change. It is evident that while the anatomical characters of some animals undergo local changes the other parts remain nearly the same; other animals are subject to slower and more evenly distributed transformations. There are analogies between biological and geological changes. When a "zone of weakness" or a region of greater strain—or whatever it may prove to be—is developed, there is more or less instability afterward, and these are the regions that are subject to greatest change while other portions remain relatively stable. So when the tendency to vary has begun in some portion of an animal there is no knowing where it will end. Other animals do not seem to have any very plastic parts, but changes progress more slowly and uniformly. It is evident that neither conservatism nor extreme plasticity preserve races from extinction.

So far as we know the Leptictidæ appear to be rather conservative, though varying considerably within certain limits. The present specimens differ so much, that it is more convenient to consider them as different species, which I think they really are. If all the intermediate varieties should be found, which is unlikely to happen, the species can be easily united.

The beds in which the fossils occur are more than 700 feet in thickness, and they have a strong dip (20° or more) to the south and southwest. They are fine-grained with local bands and lenses of sand or small gravel. There are a few fair-sized pebbles. The deposit is light gray, with a buff tint when viewed from a little distance. A large portion of the material is volcanic dust. All through the formation, at intervals, are nodules, which are arranged in bands. In places this nodular material forms strata. The nodules, as a rule, are hard, and in them most of the fossils were found.

This interesting little area is situated north and a little east of Dillon, at a distance of about sixteen miles. It is north of the Bighole River, and forms a small portion of the bench, or foothill country, of the southeastern slope of McCarty's Mountain, where the bench borders the river valley. It is in Madison County. It is about a half-mile in length north and south and about one half that distance east and west. It is sharply distinguished, from the rocks which surround it on three sides, by its color and manner of weathering. On the north is an area of basalt perhaps about equal in area. This and the Tertiary deposits lie side by side at the same level, and there are fragments of basalt in the lower portion of the White River Beds. On the east, are the shales and sandstones of the Upper Cretaceous. On the south, is the river valley, and on the west, sand and gravel benches, which are probably of later date than the Lower White River.

The beds are imperfectly stratified — at least in some portions — though on the whole they are inclined to be rather massive. At a little distance the dip can be readily distinguished. As before stated, the greater portion of these beds is soft, and the product of their weathering is instructive, as it shows how material may be transported by water and deposited without regular assortment of material or stratification. The water which descends from this area at the time of heavy rains, or when snow is quickly melted, has formed a large alluvial cone immediately at the foot of the Tertiary hills. This is broadly spread out on the river bottom below, and by its peculiar color, its area can be readily distinguished at a distance.

The following, so far as determined, are the genera found in these beds: *Testudo, Helodermoides, Xenotherium, Peratherium, Ictops, Cylindrodon, Ischyromys, Palæolagus, Hyænodon, Limnenetes, Agriochœrus, Titanotherium, Colodon, Hyracodon,* and *Mesohippus.* Others are doubtful, or have not been sufficiently cleared from the matrix for certain determination.

About two miles west of here is a small exposure of a little different character of strata. From here only two specimens were obtained, a *Colodon* and an apparently new rodent.

Besides this especially favored locality other places have been found, which have yielded interesting White River fossils. Some of them have been mentioned in previous articles. Among the new localities found are those at (*a*) Cañon Ferry, near the Missouri River east of Helena, (*b*) between Prickly Pear Creek and the Missouri River northeast of Helena, and (*c*) near Dogtown Mine near the wagon road from Three Forks to Boulder. At Cañon Ferry the most of the fossils were from the Oreodon horizon; though the beds a little to the north and northeast probably belong in part to the Titanotherium horizon. With one or two exceptions, the fossils from the other localities above mentioned, belonged to the lower beds.

ICTOPS.

The type of *Ictops* is *I. dakotensis.* It was found in the Bad Lands of White River, Dakota, in 1866, and was described by Leidy in 1868. I quote from Leidy's description.

"*Ictops dakotensis.* This name is founded on a small fragment of a skull which was obtained with the preceding [*Leptictis haydeni*]. At first the specimen was supposed to belong to the same animal as the former. It clearly indicates a skull of nearly the same size and shape as that of *Leptictis.*

"The fragment consists of a portion of the face, containing the remains of most of the molar teeth. The face appears to have had nearly the same form and construction as in *Leptictis*, and the forehead exhibits traces of the two peculiar ridges defining the upper part of the temporal fossa in the latter.

"The remains of the molars consist of the posterior six. The second premolar appears to have been a two-fanged, conical crowned tooth, as in *Leptictis.* The third premolar has a trihedral crown, inserted by three fangs, whereas in *Leptictis*, as in the preceding tooth, it has a simple conical crown with a pair of fangs.

"The crown of the third premolar of *Ictops* is composed of three principal lobes, two external and the third internal. The four back molars have the same relative position and size as regards one another as in *Leptictis*, but they do not project abruptly beyond the premolars externally as in this. Their crowns, so far as can be ascertained, appear to have had the same construction as in the third premolar.

"The space occupied by the back six molars in *Ictops* is ten lines, being a little more than *Leptictis.*"

Leidy called these two genera "insectivorous mammals, which appear to be peculiar, but related to the hedge-hogs."[1]

In his Extinct Mammalian Fauna, p. 351, Leidy describes *Ictops* a little more fully, and figures what is undoubtedly the type (Plate XXVI., Figs. 29 and 30).

---

[1] *Proc. Acad. Nat. Sci. Philad.*, 1868, p. 316.

In his Tertiary Vertebrata, p. 265, Cope, after the discovery of a skull and mandible of *Ictops* (*Palæictops*) *bicuspis* and a fragment of a mandible of *I. didelphoides*, gave the following generic characters. Dental formula $I\frac{3}{2}$, $C\frac{1}{1}$, $Pm\frac{4}{4}$, $M\frac{3}{3}$. "Third superior premolar tooth with two external and an internal cusp; fourth premolar like the true molar, with two external tubercles, an internal tubercle, and a posterior cingulum. Fourth inferior premolar with an internal and a well developed anterior tubercle; the anterior tubercle of the true molars median in position, and much smaller than the internal tubercle. Heels of molars with elevated cusps. Orbits not closed posteriorly. Coronoid process of mandible well developed. Inferior margin of mandible not inflected."

With regard to the systematic position Cope says, "*Ictops* agrees very closely with *Didelphys*. The fourth superior premolar has an internal cusp, which is wanting in *Didelphys*, and the inferior border of the mandible is not inflected. There are also but three superior incisors on each side. Under these circumstances I prefer to refer this genus to the *Bunotheria* rather than to the *Marsupalia*, but whether its proper place is in the Creodont or Insectivorous subdivisions I cannot yet determine."

On page 800 of the Tertiary Vertebrata Cope says that *Leptictis*, *Ictops*, and *Mesodectes* belong to a distinct division from *Peratherium* and *Domnina* and that this division is perhaps of ordinal value, but it remains uncertain on account of the incompleteness of the specimens.

Species of Ictops.

Ictops didelphoides Cope.

Bull. U. S. Geol. Surv. Ter., VI., p. 192. Figured in Cope's Tertiary Vertebrata, Pl. XXV*a*, fig. 9.

It is represented by a fragment of a lower jaw with three teeth. This may not be *Ictops* at all, and if so it is of very little use for our purpose.

Ictops acutidens Douglass.

This species was found in the Titanotherium Beds of Pipestone Springs, Montana, and described by Douglass.[1] It is represented by an upper jaw with the five posterior teeth, the lower jaws with the molar teeth and one premolar — the anterior portions of both rami absent — a lumbar vertebra, a femur, part of a tibia, an astragalus, and a calcaneum. It is a rather young individual, but probably nearly full grown. In my paper I gave a general description, but did not give a clear diagnosis of the distinguishing specific characters as they were not then known, the only species really available for comparison being *Ictops dakotensis* of the Oreodon Beds of the plains.

---

[1] Fossil Mammalia of the White River Beds of Montana, *Trans. Am. Phil. Soc.*, N. S., Vol. XX., p. 245. Reprint p. 9.

Dr. Matthew found, in the same beds as the type, another specimen, which added a little to the features shown by the type. He gives more definitely the characters which are supposed to distinguish this from other known species.[1]

"Dimensions fifteen per cent. less than any of the *Leptictidæ* of the Oreodon Beds. First upper premolar one-rooted, two-rooted in *I. dakotensis* and *bullatus* and *Leptictis haydeni.* Supra-temporal crests widely separated anteriorly and convergent posteriorly, instead of close together and parallel as in the latter species. Upper molars and $\mathrm{P}^{\underline{4}}$ more constricted between the inner and outer cusps than in any described Leptictid; cusps somewhat higher and last molar less reduced than in any later species."

With regard to the last character, I would say that I have the type specimen before me as I write, and the last upper molar is much smaller than $\mathrm{M}^{\underline{2}}$, and much smaller than the one represented in Matthew's illustration, fig. 4, in the paper from which I quote.

Ictops Thompsoni Matthew.

Bull. Amer. Mus. Nat. Hist., Vol. XIX., 1903, p. 207, fig. 5.

This species was found in the same beds as *I. acutidens* at Pipestone Springs. According to Matthew it is distinguished by the following characters:

It is allied to *I. acutidens* but is smaller and has more compressed teeth. "The metacone on all the molars is decidedly smaller than the paracene; in *I. acutidens* they are nearly, and in other Leptictidæ quite, equal in size on $\mathrm{M}^{\underline{1-2}}$. The protocenes on $\mathrm{P}^{\underline{4}}$ and $\mathrm{M}^{\underline{3}}$ is more compressed antero-posteriorly, and the constriction between it and the outer cusps is more marked than in *I. acutidens.* The hypocene is smaller on $\mathrm{M}^{\underline{1}}$ and $\mathrm{M}^{\underline{2}}$ and absent on $\mathrm{M}^{\underline{3}}$ and $\mathrm{P}^{\underline{4}}$. The trittocene of $\mathrm{P}^{\underline{4}}$ is smaller than in *I. acutidens.* All of these distinctions are exaggerations of the differences between *I. acutidens* and the Leptictidæ of the Oreodon Beds."

Ictops montanus sp. nov.

(Plate XXII., Figs. 1, 2, 3 and 4.)

Carnegie Museum, No. 1020.

From the Titanotherium Beds near McCarty's Mountain, Montana.

This is a finely preserved skull. It lacks the end of the snout, a portion of the brain-case, and the zygomatic arch on one side.

Principal Characters. — *Skull quite broad and heavy behind with fairly large brain case. In front of the orbits a gradual constriction from all sides to form the rather*

---

[1] Bull. Amer. Mus. Nat. Hist., Vol. XIX., p. 205.

long muzzle. Zygomatic arches deep — broad as seen from the side. Post-glenoid process long and inclining forward toward the lower end. Squamosal extending downward in a broad mastoid process outside of the external auditory meatus. Depression at anterior portion of zygomatic arch rather deep. Anterior cusp of P^{4} *small and low.*

General Description.

Dentition. — In this specimen the incisors and canines are not preserved; the premolars and molars on the right side are well preserved, also the last five teeth on the left side.

P^{1} is a small, simple, laterally compressed, one-rooted tooth, slightly curving backward toward the point. The diastema behind this tooth is about three times the length of the tooth.

P^{2} is a little larger, is two-rooted, has a sharply-pointed protocone and a minute posterior cusp.

P^{3} is three-rooted, has a minute anterior cusp, a protocone larger than that in P^{2}, and a well developed posterior cusp which is, except at its point, connate with the higher protocone. This tooth has a well developed but not very large conical deuterocone. There is a trace of a cingulum on the exterior and posterior portions. On all the teeth posterior to P^{2}, the antero-external is higher than the postero-external cusp.

P^{4} is nearly like the molars, is smaller than M^{1} and M^{2} but slightly larger than M^{3}. It has a small, low, anterior basal cusp which is only slightly above the alveolar border. The tritocone is separated from the protocone little if any more than in P^{3}, but is much nearer equal to it in size. The posterior cusp on the deuterocone is minute.

M^{1} differs from P^{4} in having a lower antero-external cusp, which is more separated from the postero-external one, in having a cingulum with minute outer anterior and posterior basal cusps, and in having a somewhat larger, yet small, postero-internal cusp. The tooth is also wider transversely than P^{4}.

M^{2} differs very little from M^{1}.

M^{3} is smaller, has a reduced postero-external cusp, and has no postero-internal one.

Description of Skull.

The occiput is broad, medially vertical, and sub-semicircular as seen from behind. The height is about four fifths the width — the exact proportions being 18 : 22 millimeters. The foramen magnum is large and has a heart-shaped outline. It is about one third the width of the occiput, and nearly half the height. It extends for nearly half its height above the occipital condyles, so that the latter are far apart superiorly, but approach each other and are nearly or quite confluent below on the lower portion of the skull; thus, apparently indicating an angular position of the skull with reference to the cervicals. Above the foramen magnum, on the median line of the skull, a median ridge — the culmination of a median convexity — ascends to the crest of the occiput. Between this median convexity and the foramen magnum on the inside, and the lambdoid ridges on the outside, is a somewhat uneven depression. The lambdoid ridges are somewhat oblique, the lower portions being a little in advance of the foramen magnum. The posterior lower portions of the squamosal form a plate or long process outside of the periotic bones, both of which are preserved in the specimen. There are, in the collection, two skulls, which have the posterior lower portion well preserved. No tympanic bullæ are present but the form of the skull here makes it reasonably certain, I think, that the animal had large auditory bullæ. They may have been cartilaginous, or ossified but very thin, and have separated from the skull before its inhumation. The lower surface of the basioccipital is broadly convex just in front of the occipital condyles, and narrows anteriorly. This continues in a still narrowing convexity on the basisphenoid, and as a small narrow ridge on the presphenoid. The post-glenoid processes are rather long, projecting some distance below the zygzomatic arches and curving forward. The glenoid surface is triangular and slightly convex. The pterygoids have, at the posterior portion, two small triangular winglike processes which are directed outward. The opening of the posterior nares is in a plane with the last molars. The palate ends on the median posterior border in a point or lobe. The border on each side of this is symmetrically rounded. There are foramina in the palatines just posterior and internal to the last molar. The anterior portion of the maxillo-palatine foramen is between the fourth premolars. The palate is slightly arched in the type specimen. The anterior part of the snout is broken off, but the first premolar tooth is present on one side.

The face is concave in front of and below the orbit, the depression invading the anterior portion of the zygomatic arch. In front of this the muzzle is nearly semicircular in section, and it tapers gradually forward. The nasals are long and narrow. They have a short contact with the frontals. The zygomatic arches are broad and are about equally made up of the malar and squamosal portions; though the former is a little broader vertically, than the latter. The posterior process of the malar extends to the glenoid surface. The lachrymals appear nearly circular as seen from the side. They are small and appear as a little narrow crescent outside the orbit. The fronto-maxillary sutures extend obliquely upward and forward from the orbit.

On the top of the skull on the anterior portions of the frontals are two oblong convexities extending backward from the anterior points of these bones and slightly diverging posteriorly. Between these along the frontal suture is a longitudinal concavity. The posterior portions of the frontals are flat or slightly concave. The greater portion of the parietals is broken away showing a cast of the brain-case. On the frontal the supra-temporal ridges are hardly distinguishable. On the posterior portion of the parietals they can be plainly seen. They are a considerable distance apart but converge slightly forward. The parieto-temporal suture is nearly horizontal. There are no post-orbital processes and the post-orbital constriction is slight.

Ictops intermedius sp. nov.

Carnegie Museum Collection, No. 1019.

This species is represented by the skull of an old individual with the lower jaw. The snout is gone, but it is in part restored in plaster from the impression on the rock. It was found in the same beds with *Ictops tenuis* to be described later, though at a little higher level, in the Titanotherium Beds of McCarty's Mountain, north of Dillon, in Montana.

Principal Characters. — *The skull is smaller than that of* Ictops montanus *and less robust. Though the skulls are similar throughout, yet there are differences, either slight or more pronounced in nearly every part. The most noticeable are the following: In* I. intermedius *the zygomatic arches are much more slender, the post-glenoid processes smaller and shorter, the mastoid process does not extend downward so far and is entirely different in form, the posterior portion of the skull is narrow, and the foramen magnum smaller. The teeth are shorter antero-posteriorly but fully as wide.*

Detailed Comparison.

The upper teeth are too much worn for accurate comparison.

The Skull. — Measuring from the anterior of $P^{\underline{1}}$ to the occipital condyles this skull is 90 per cent. of the length of that of *I. montanus.* The width at the post-glenoid processes is 86 per cent. The width of the occiput nearly 82 per cent., the depth of the anterior portion of the zygomatic arch 71 per cent., and of the posterior 66 per cent. The occipital region besides being smaller was apparently more convex, but it is somewhat injured in the present specimen so one cannot be sure. The palate views of the skulls are much alike, except in the size of the different parts. The depression at the anterior portion of the zygomatic arch is much shallower than in *I. montanus,* or in *I. tenuis,* which are described in this paper. The zygomatic arch is slenderer than in any other specimen I have examined except, perhaps, *I. acutidens.* This specimen has no convexities on the top of the skull above the orbits like those in *I. montanus.* The post-orbital constriction is slightly more noticeable than in the latter species. The post-glenoid process is small and short. The mastoid process of the squamosal is quite long antero-posteriorly but does not extend down so far and curve as much as it does in *I. montanus.*

The Mandible.—The lower jaw is fairly deep and heavy. All the teeth are preserved. There are three incisors on each side, of nearly equal size. They are semi-procumbent and their arrangement is nearly fore-and-aft parallel to the long axis of the jaw.

The canine is quite long, straight, and slender, and, like the incisors, is semi-procumbent, being directed more forward than upward. It is close to the third incisor; there being no space between them.

$P_{\overline{1}}$ is small, apparently one-rooted, is directed forward, and is low crowned.

$P_{\overline{2}}$ is much larger, more erect, yet directed slightly forward. It has a hint of a heel or small basal cusp.

$P^{\underline{3}}$ is nearly erect, has a small posterior cusp and a rudimentary anterior one.

$P^{\underline{4}}$ has a distinct anterior cusp and a well developed basal heel.

The molars are about equal in size but are so worn that the relative proportions of their various cusps cannot be determined with certainty.

The horizontal ramus of the mandible is moderately deep and heavy. It deepens gradually from the incisors backward to the last molar. The angle is injured. The masseteric fossa is deep and the anterior border of the edge of the ascending ramus is a narrow ridge.

Ictops tenuis sp. nov.

Carnegie Museum Collection, No. 1021.

An adult, but not old.

Found in Titanotherium Beds southeast of McCarty's Mountain near the same level as the type of *Ictops intermedius,* and somewhat higher than that of *I. montanus.* Of this specimen we have the anterior portion of the skull with the snout complete, the left ramus of the mandible lacking the top of the coronoid process, a radius, parts of the ulna and tibia, fragments of ribs, and other bones.

PRINCIPAL CHARACTERS.—*This is larger than either of the specimens previously described. The most noticeable differences besides the greater size are the greater width of the palate between the teeth and the much greater width at the post-orbital constriction. The teeth are wider in proportion to the length than in* I. montanus. *The palate, though 40 per cent. wider at* $M^{\underline{2}}$, *is nearly the same width at* $P^{\underline{1}}$ *as that of* I. montanus. *The muzzle is* *slender in proportion to the size of the skull. The anterior portion of the zygomatic arch is proportionally more like that of* I. intermedius. *The skull is one fifth broader than in the latter between the orbits and one third broader at the post-orbital constriction. Though the mandible is nearly one third longer, it is no deeper at the last molar.*

DETAILED DESCRIPTION AND COMPARISONS.

Dentition.—No upper incisors are preserved. On each side are alveoli for the third incisors, but it does not appear that there were functional first and second incisors. If there were, they were separated from $I^{\underline{3}}$ by a diastema, and were not crowded like the corresponding lower teeth. The canine was small. Only the root is preserved. All the teeth on the right side anterior to $P^{\underline{3}}$ are gone and appear to have been shed when the animal was young, as the alveoli are more or less nearly obliterated.

$P^{\underline{1}}$ is larger than in *I. montanus* but it is a simple, one-rooted, laterally compressed tooth. The diastema between it and $P^{\underline{2}}$ is the same. $P^{\underline{2}}$ is about the same in both specimens. $P^{\underline{3}}$ and $P^{\underline{4}}$ are longer in the present specimen and $P^{\underline{4}}$ is wider. As in *I. montanus* the anterior cusps of the molars are higher than the posterior ones. The molars have nearly the same antero-posterior diameter in the two species, but in *P. tenuis* the transverse diameter is much greater, and the inner portion of the tooth is very narrow. Taking Matthew's figure of *I. thompsoni* as a basis for measurement the teeth of the present specimen are even wider in proportion to the length than in that species. The last molar is absent from both sides.

The snout is very slender as compared with the size of the skull. The skull is very broad at the zygomatic arches, but narrows rapidly at their anterior portions and just in front of the orbit. The palate is broad behind and narrows gradually almost to a point in front. The posterior narial opening is in the plane of the last molars. There is a median point at the posterior portion of the palate. Though the skull was larger, the depth of the malar portion of the zygomatic arch is about the same as in *I. montanus.* The depression on the face at the anterior root of the arch has about the same depth but is smaller, leaving a heavier ridge between that and the orbit. The nasals are long and slender and are broadest at the anterior portions. The skull is broader on top than in any other specimen of *Ictops* that I have seen.

The Mandible. — The greater portion of the left side of the mandible is present. The coronoid process and the condyle are gone, and the angle is probably not quite complete.

Portions of the first incisors, canine, and second and third premolars are preserved. As in *I. intermedius* and *I. major* there are no diastemata in the lower jaw.

In the upper jaw there is a short interval between the canine and $P^{\underline{1}}$, a quite long one between $P^{\underline{1}}$ and $P^{\underline{2}}$, and a short one between $P^{\underline{2}}$ and $P^{\underline{3}}$. The mandible is deepest at $M_{\overline{1}}$. The anterior ridge of the ascending ramus is heavier and broader than in *I. intermedius.* All the mandibles of the different specimens have two mental foramina; but, as will be seen by the illustrations, they have a little different position in each.

Skeleton.—Nearly a whole ulna and the lower part of the radius are preserved They were apparently nearly equal in size. The radius is nearly 4 cm. in length. The olecranon is .8 cm. There is a longitudinal convexity on the shaft of the ulna giving the bone an angulate appearance.

One of the anterior dorsal vertebræ is preserved. It has a long spine, which is very much inclined backward.

ICTOPS.

Carnegie Museum specimen, No. 812.

This is the larger portion of a skull but it is much crushed and distorted so that but few of its characters can be definitely ascertained.

This skull was found in beds of sandy clay west of Three Forks, Montana, associated with *Titanotherium* and a little Oreodont. The beds are different lithologically from those of the same region in which *Limnenetes platyceps*, *L. anceps*, *Agriochœrus minimus*, *Trigenicus socialis*, *Mesohippus latidens* and associated *Titanotherium* remains were found. It is uncertain whether these beds are exactly contemporaneous with those containing the *Ictops* skull or not, but they must be nearly so. This skull is quite robust. The zygomatic arch is heavier than in any other specimen in the collection. The post-glenoid process is fairly long. The most noticeable feature is the wide interval which separated the supra-temporal ridges. They converge backward to within .6 cm. of the crest of the occiput and back of this diverge, becoming continuous with the lambdoid ridges. Where nearest they are 1 cm. apart. The occiput was broad, the nasals slender.

Ictops Major sp. nov.

Carnegie Museum specimen, No. 1022.

Of this specimen we have the upper dentition back of $P^{\underline{2}}$, a large portion of the mandible with all the lower teeth except $I_{\overline{1}}$, parts of the dorsal vertebræ, the sacrum, part of the pelvis, portions of the tibiæ, two caudal vertebræ, two phalanges, and other small fragments of the skeleton. The specimens were found in the Titanotherium Beds southeast of McCarty's Mountain, but at a lower level than the specimens above described. This represents the largest *Ictops* found in the beds at this place. The inferior dental series is 32 per cent. (nearly $\frac{1}{3}$) larger than that of *I. intermedius* and 10 per cent. larger than *I. tenuis*.

DENTITION.

Superior Dentition. — The width of P^3 is about two-thirds its length. In *I. tenuis* it is about one-half. The posterior cusp is more distinct from the protocone than in *I. montanus*. There is a cingulum on the posterior outer portion of the tooth.

P^4 has a low and minute but distinct anterior basal cusp, and a strong cingulum on the posterior outer portion. The protocone is a little higher than the cusp behind it. Both are lens-shaped in section and rather blunt pointed as seen from the side. The tooth has minute traces of anterior and posterior intermediate cusps. The posterior interior cusp appears as a cingulum-like ledge.

The molars have distinct cingula on the outside tending to form anterior and posterior outer basal cusps, except on the posterior of M^3. There is a minute cingulum on the anterior portion of the inner cusp in M^1 and the posterior inner cusp is small but well developed. M^2 has also an anterior cingulum but the posterior cusp is smaller than on M^1. M^3 is smaller than the other molars and its posterior outer cusp (metacone) is minute. It has a trace of the posterior inner cusp.

Inferior Dentition. — The first incisor is wanting. The other incisors and the canine are arranged in an antero-posterior row in line with the premolars and molars. I_2 and I_3 are spatulate, not much unlike the lower incisors of modern ruminants. I_2 is larger than I_3.

The canine has a higher crown than the incisors, but is narrow toward the top, instead of expanding like the incisors.

P_1 is one-rooted and it inclines forward, but less so than the canine.

P_2 is two-rooted and has a small heel. The protoconid is quite high and nearly erect.

P_3 has anterior and posterior cusps on the protoconid of nearly equal size and height, and a minute basal heel.

On P_4 the anterior cusp is larger than on P_3. The outer principal cusp is larger and higher than the inner one. On the heel the outer cusp is higher and larger than the inner one, and this in turn is larger than the median one.

M_1 differs from P_4 in having the anterior cusp higher and more confluent with the two principal cusps which are more nearly equal in size and height and are flatter behind, in the outer cusps of the heel being more nearly even, and in the median posterior cusp being larger. On M_3 the posterior cusp on the heel is higher than the other two.

Most of the fragments of the skeleton are too imperfectly preserved to admit of accurate description. Portions of five of the lumbar vertebræ are still united and in position. The centra are injured. Three of them are 2 cm. in length.

The tail was long and heavy judging by two vertebræ from near the anterior portion, and two others farther back. They are as broad as the lumbars and the two measure 2 cm. in length. Two other caudals are preserved; one 1.15 cm. in length, apparently from near the middle, and one 1 cm. in length from near the end.

A metacarpal was found at the same place, but it is not certain that it belongs to this specimen. One median and one ungual phalanx are also preserved. The latter has a short heel on the dorsal surface and a small one on the plantar portion.

The species of *Ictops* thus far secured from the Titanotherium Beds are:

Ictops thompsoni, I. intermedius, I. montanus, I. acutidens, I. tenuis and *I. major.*

The beds are in some places at least several hundred feet in thickness, being several times thicker than in the type locality, but as yet different faunal horizons have not been distinguished. At least three of the species have come from levels not differing greatly in height, probably less than 100 feet, yet of the lapse of time between their deposition we know nothing.

In size the species rank as follows: (1) *Ictops thompsoni*, smallest, (2) *I. intermedius*, (3) *I. montanus, I. acutidens*, (4) *I. tenuis* and (5) *I. major.*

SPECIES OF ICTOPS FROM MONTANA.

I. *Ictops acutidens.*	II. *Ictops montanus.*	III. *Ictops intermedius.*	IV. *Ictops tenuis.*	V. *Ictops major.*
$P^{\underline{3}}$ has four distinct and separate cusps.	$P^{\underline{3}}$ anterior cusp very small. Protocone and postero-external cusp connate.	$P^{\underline{3}}$ cusps low and blunt; the anterior one hardly distinguished as a cusp.	$P^{\underline{3}}$ protocone high; the three other cusps low and small.	$P^{\underline{3}}$ much as in last but larger and cusps more massive and not so acute.
$P^{\underline{4}}$ tritocone larger but not so high as protocone. Two small intermediate cusps between outer and inner ones. A strong outer cingulum, and anterior and posterior outer cingular cusps.	$P^{\underline{4}}$ protocone much higher than tritocone; postero-external cusp small; cingulum weak and antero-external cusp smaller than in I.		$P^{\underline{4}}$ protocone decidedly higher and larger than tritocone; antero-external basal cusp small. Cingulum on anterior and posterior outer portions of tooth.	$P^{\underline{4}}$ anterior and posterior outer cusps small. Cingulum nearly surrounding tooth; protocone higher than tritocone.
$M^{\underline{1}}$ strong postero-internal cusp, strong cingulum on outside. Length of tooth nearly equals width.	$M^{\underline{1}}$ postero-external cusp not so large as in I.; cingulum not so strong; tooth wider in proportion to length.		$M^{\underline{1}}$ postero-external cusp small; cingulum quite strong; tooth very wide in proportion to length.	
$M^{\underline{3}}$ much smaller than $M^{\underline{2}}$.	$M^{\underline{3}}$ proportionally larger than in I.	$M^{\underline{3}}$ proportionally larger than in I. or II.		$M^{\underline{3}}$ about as in I.
Zygoma not heavy.	Zygoma heavy.	Zygoma comparatively slender.	Zygoma heavy.	
	Post glenoid processes large.	Post-glenoid processes much smaller than in II.		

Measurements of Species of Ictops.

	I. montanus. mm.	*I. intermedius.* mm.	*I. tenuis.* mm.	*I. acutidens.* mm.	*I. major.* mm.	*I. thompsoni.*[1] mm.	*I. dakotensis.*[1] mm.
Length of skull back of P^1	48.5	45					
Width of skull at P^2	8	6	7.6				
Width of skull at post-orbital constriction	13	12	16				
Width of occiput	20	18					
Width of occipital condyles	15	13					
Width of palate at P^2	5.5	6	6.5				
Width of skull at front of glenoid surface	25	24	33				
Length of molar-premolar series	23	22	28				
Length of premolar series	15.5	15.5	21				
Length of molar series	7.5	6.5	7		10		
Length of molars and P^3 and ^{4}	14	12	14		18	9.3	
Length of P^1	1.3		2				
Length of P^2	2.1		2.8				
Length of P^3	3.5	2.5	3.8	3.5	5		
Length of P^4	3	2.2	3.1	3.3	3.8		
Width of P^4	2.8	3.3	2.9	3.3	3.4		
Length of M^1	2.5	2.2	2.2	3	3.6	2.7	3.3
Width of M^1	3.5	3.5	4.2	3.8	4.3	3.9	4
Length of M^2	2.2	2.2	2.2	2.2	3.5		
Width of M^2	3.8	4	4	4.2	5		
Length of M^3	2	2		1.5	2	1.5	
Width of M^3	3	3		3	4	3.6	
Depth of mandible under M$_{\overline{3}}$		5	5.2	4.5	5.7		
Length of lower dental series		25	29		32		
Length of lower molar series		7		8.5	10		
Length of M$_{\overline{1}}$		2.5		2.5	4		
Length of M$_{\overline{3}}$		3	3	2.5	3.2		
Length of femur					45		

[1] According to Matthew, *I. dakotensis* measured from Leidy's figure.

In width of molars in relation to length: (1) *I. tenuis,* widest in proportion to length, (2) *I. intermedius, I. thompsoni,* (3) *I. montanus,* (4) *I. major, I. acutidens.*

In development of cingulum on cheek teeth: (1) *I. intermedius?* least, (2) *I. tenuis,* (3) *I. montanus, I. acutidens, I. major.*

In robustness of zygomatic arch: (1) *I. acutidens* least, (2) *I. intermedius,* (3) *I. tenuis,* (4) *I. montanus.*

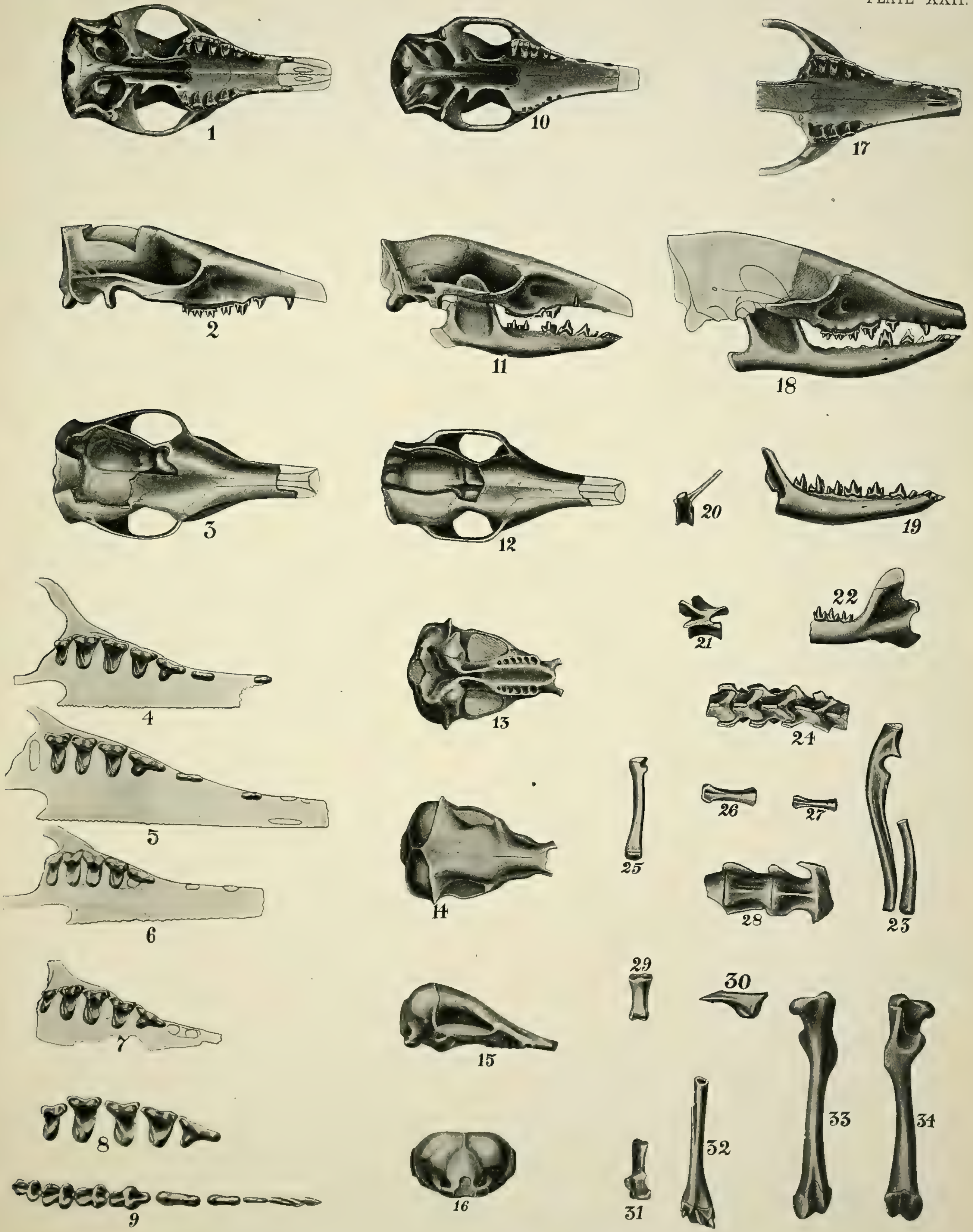
From what I have seen of the Leptictidæ of the Oreodon horizon I think that in all these species from the Titanotherium beds of Montana, unless it be *I. major,* the teeth are proportionately smaller.

Explanation of Plate XXII.

ALL FIGURES NATURAL SIZE.

Fig. 1. *Ictops montanus.* Skull, palate view.
Fig. 2. " " " side view.
Fig. 3. " " " top view.
Fig. 4. " " Upper teeth. Crown view.
Fig. 5. *Ictops tenuis.* " " " "
Fig. 6. *Ictops intermedius.* " " " "
Fig. 7. *Ictops acutidens.* " " " "
Fig. 8. *Ictops major.* " " " "
Fig. 9. " " Lower " " "
Fig. 10. *Ictops intermedius.* Skull, palate view.
Fig. 11. " " Skull and mandible, side view.
Fig. 12. " " Skull, top view.
Fig. 13. *Xenotherium unicum.* Skull, palate view.
Fig. 14. " " " top view.
Fig. 15. " " " side view.
Fig. 16. " " " rear view.
Fig. 17. *Ictops tenuis.* Anterior portion of skull, palate view.
Fig. 18. " " " " " " and mandible, side view.
Fig. 19. *Ictops major.* Right ramus of mandible.
Fig. 20. *Ictops tenuis.* Dorsal vertebra.
Fig. 21. *Ictops acutidens.* Lumbar vertebra.
Fig. 22. " " Left ramus of mandible, posterior portion (type specimen).
Fig. 23. *Ictops tenuis.* Ulna and part of radius.
Fig. 24. *Ictops major.* Lumbar vertebræ.
Fig. 25. " " (?). Metapodial.
Figs. 26 and 27. *Ictops major.* Caudal vertebræ.
Fig. 28. *Ictops major.* Anterior caudal vertebræ.
Fig. 29. " " Phalanx.
Fig. 30. " " Ungual phalanx.
Figs. 31 and 32. *Ictops acutidens.* Calcaneum, astragalus and part of tibia and fibula.
Figs. 33 and 34. " " Femur.

Ictops montanus. Figs. 1, 2, 3 and 4.
Ictops intermedius. Figs. 6, 10, 11 and 12.
Ictops tenuis. Figs. 5, 17, 18, 20 and 23.
Ictops acutidens. Figs. 7, 21, 22, 31, 32, 33 and 34.
Ictops major. Figs. 8, 9, 19, 24, 25, 26, 27, 28, 29 and 30.
Xenotherium unicum. Figs. 13, 14, 15 and 16.



LOWER WHITE RIVER MAMMALS. *ICTOPS* AND *XENOTHERIUM.*

Publications of the Carnegie Museum. Serial Nos. 37, 39, 40, and 41.

MEMOIRS
OF THE
CARNEGIE MUSEUM.

VOL. II. NOS. 6, 7, 8, AND 9.

W. J. HOLLAND, EDITOR.

6. THE OSTEOLOGY OF DIPLODOCUS MARSH,

WITH SPECIAL REFERENCE TO THE RESTORATION OF THE SKELETON OF DIPLODOCUS CARNEGIEI HATCHER, PRESENTED BY MR. ANDREW CARNEGIE TO THE BRITISH MUSEUM, MAY 12, 1905.

BY W. J. HOLLAND.

7. THE OSTEOLOGY OF PROTOSTEGA.

BY G. R. WIELAND.

8. NEW SUILLINE REMAINS FROM THE MIOCENE OF NEBRASKA.

BY O. A. PETERSON.

9. NOTES ON OSTEOLOGY OF BAPTANODON WITH A DESCRIPTION OF A NEW SPECIES.

BY C. W. GILMORE.

PITTSBURGH.
PUBLISHED BY THE AUTHORITY OF THE BOARD OF TRUSTEES OF THE
CARNEGIE INSTITUTE.
MARCH, 1906.

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 6.

THE OSTEOLOGY OF DIPLODOCUS MARSH.

With Special Reference to the Restoration of the Skeleton of Diplodocus Carnegiei Hatcher, Presented by Mr. Andrew Carnegie to the British Museum, May 12, 1905.

By W. J. Holland, LL.D.

In the first volume of the Memoirs of the Carnegie Museum, the late Mr. J. B. Hatcher gave an extended account of the Osteology of Diplodocus, based upon two specimens contained in the paleontological collections of the Carnegie Museum, numbered respectively 84 and 94 (Carnegie Museum Catalogue of Vertebrate Fossils), supplemented in part by information derived from the original descriptions of the late Professor O. C. Marsh, and the description of the pelvis and portions of the caudal vertebræ published by Professor Henry Fairfield Osborn in the Memoirs of the American Museum of Natural History, Vol. I., Part V. In the second volume of the Memoirs of the Carnegie Museum Mr. Hatcher published a brief paper, which he entitled "Additional Remarks on Diplodocus."[1] Since the publication of the foregoing papers the Carnegie Museum has secured a large quantity of additional material, consisting of two more or less imperfect skeletons, which are designated in

---

[1] Memoirs Carnegie Museum, Vol. II., p. 72.

Note. — The writer desires to express his sincere thanks to Professor Henry Fairfield Osborn and Dr. W. D. Matthew of the American Museum of Natural History, to Dr. Theodore Gill, Dr. George P. Merrill, Mr. C. W. Gilmore, and Mr. J. W. Gidley of the United States National Museum, and to Dr. Smith Woodward, Dr. C. W. Andrews, and Dr. G. A. Boulenger of the British Museum, for valuable suggestions and for allowing him to study the material contained in the great collections under their charge.

AF

the Catalogue of Vertebrate Fossils of the Museum as Nos. 307 and 662. Moreover, a restoration of an entire skeleton has been prepared at the command and expense of Mr. Andrew Carnegie, at the suggestion of King Edward VII., of England, and this restoration was set up and installed by the writer in the Gallery of Reptiles at the British Museum and formally turned over to the Trustees of that institution by Mr. Andrew Carnegie on May 12, 1905. The restoration was made in the laboratories of the Carnegie Museum by Mr. Arthur S. Coggeshall, the efficient Chief Preparator in the laboratory, guided and directed in his work by Mr. J. B. Hatcher until the end of June, 1904, when his illness, succeeded by his lamented death, compelled the writer to assume supervision of the task, which had not been wholly completed. The more recently acquired material and the careful studies necessitated by the work of restoration have thrown new light upon the entire subject, and it is the purpose of the writer in the following pages to briefly point out the additions to our knowledge of the skeletal structure of the genus Diplodocus which have thus been secured. At the time of Mr. Hatcher's death the entire vertebral column from the axis to the extremity of the caudal series of vertebræ, so far as they are in our possession, had been placed in position, the ribs had been attached, and the fore and hind limbs erected. The atlas and the skull had not yet been restored or placed in position, nor had a disposition been made by Mr. Hatcher of the sternal plates, nor of the singular bone provisionally described by him as a clavicle.[2] The last professional interview between the writer and Mr. Hatcher took place in the Great Hall of the Exposition Society of Western Pennsylvania, where the restored skeleton was being assembled preparatory to shipment to London, and the time was spent in discussing with Mr. Hatcher the possible position which might be assigned to the so-called "sternal plates" and the supposed "clavicle." Mr. Hatcher confessed himself to be greatly puzzled, and the writer fully shared with him in the feeling of uncertainty, which prevailed in his mind, a feeling which has not been dissipated, and for excellent reasons, as will be made clear in the following pages. With the exception of the sternal plates and the supposed clavicle, there is no longer much doubt in the mind of the writer as to the function and relative position of all the bones which have thus far been recovered. The arrangement of the bones of the fore feet was made by Mr. Hatcher as the result of careful study, and the reproduction in the British Museum represents his views. The writer is, however, inclined to think that the manus in this reproduction is not represented in quite a natural position, and is disposed to the view that the feet should hold a position somewhat less digitigrade and more plantigrade than was given to them by his late associate.

---

[2] MEMOIRS CARNEGIE MUSEUM, Vol. 1., p. 41, and Vol. II., p. 74.

THE SKULL.

Materials upon which our Knowledge of the Skull of Diplodocus is Based.

At the time when Mr. Hatcher published his first paper upon Diplodocus he made use of the words, "Unfortunately there is no skull of Diplodocus in our collections." He therefore repeated the figures and descriptions of Professor Marsh in order to make his account of the animal complete, so far as possible. One of the specimens secured for the Museum by Mr. W. H. Utterback, in Wyoming, in the year 1902 (Acc. $\frac{662}{22}$), yields the entire posterior portion of a skull in very perfect state of preservation. While the anterior portion of this skull and the lower jaws are missing, the specimen, which has been very carefully and skillfully freed from the matrix, throws a great deal of light upon the structure of the posterior portion of the skull. Both Mr. Hatcher and the writer were accorded by the authorities of the United States National Museum the fullest opportunity to examine and minutely study the two skulls upon which Professor Marsh based his description in his work upon the Dinosaurs of North America. (See Plates XXIII.–V.) These skulls were designated by Professor Marsh as specimen 1921 (U. S. N. M., No. 2672), and specimen 1922 (U. S. N. M., No. 2673). A cast of the latter, which is the more perfect specimen, was made with the consent of the officers of the United States National Museum. One half only of the external surface of this skull is thoroughly freed from the matrix. Using this half as the basis of our work, we restored the other half, using the portion of the skull belonging to the Carnegie Museum in modeling the occipital region. The skull employed in the restoration in the British Museum embodies in its outline the well-ascertained characteristics of these two skulls. Through the kindness of Professor Henry Fairfield Osborn we were enabled to secure for study a cast of the reproduction of the skull of a Diplodocus recently made by Mr. Hermann at the American Museum of Natural History. (See Plate XXVI.) This skull (A. M. N. H., No. 969) is based upon a specimen, somewhat fragmentary in character, obtained by the American Museum of Natural History, but it serves to illustrate some of the more important features of the structure under discussion. Mr. Hermann, so far as the external portions of the upper part of the skull are concerned, was unfortunately compelled to rely largely upon the figures and descriptions given by Professor Marsh, and in a few minor respects has not been quite successful in interpreting them. The restoration, though valuable, is defective, as was the original. In addition to the material mentioned above, which was at the command of the writer at the time the reproduction of the skull was prepared, there are in the possession of the American Museum of Natural History in New York the back portions of two other skulls (Nos. 545 and 694, Cat. Vert. Foss. A. M. N. H.). They both, according to Professor Osborn, represent individuals younger than the one used by him in making the restoration (No. 969), to which reference has been already made, and tend to throw light upon important points.

The Position of the Skull in Relation to the Vertebral Column.

Professor Marsh pointed out in his description of the skull the very important fact that the occipital condyle "is placed nearly at right angles to the long axis of the skull." ("Dinosaurs of North America," p. 175.) In speaking of the brain he observes, *l. c.*, p. 178, that "It differed from the brain of the other members of the Sauropoda, and from that of all other known reptiles, in its position, which was not parallel with the longer axis of the skull, as is usually the case, but inclined to

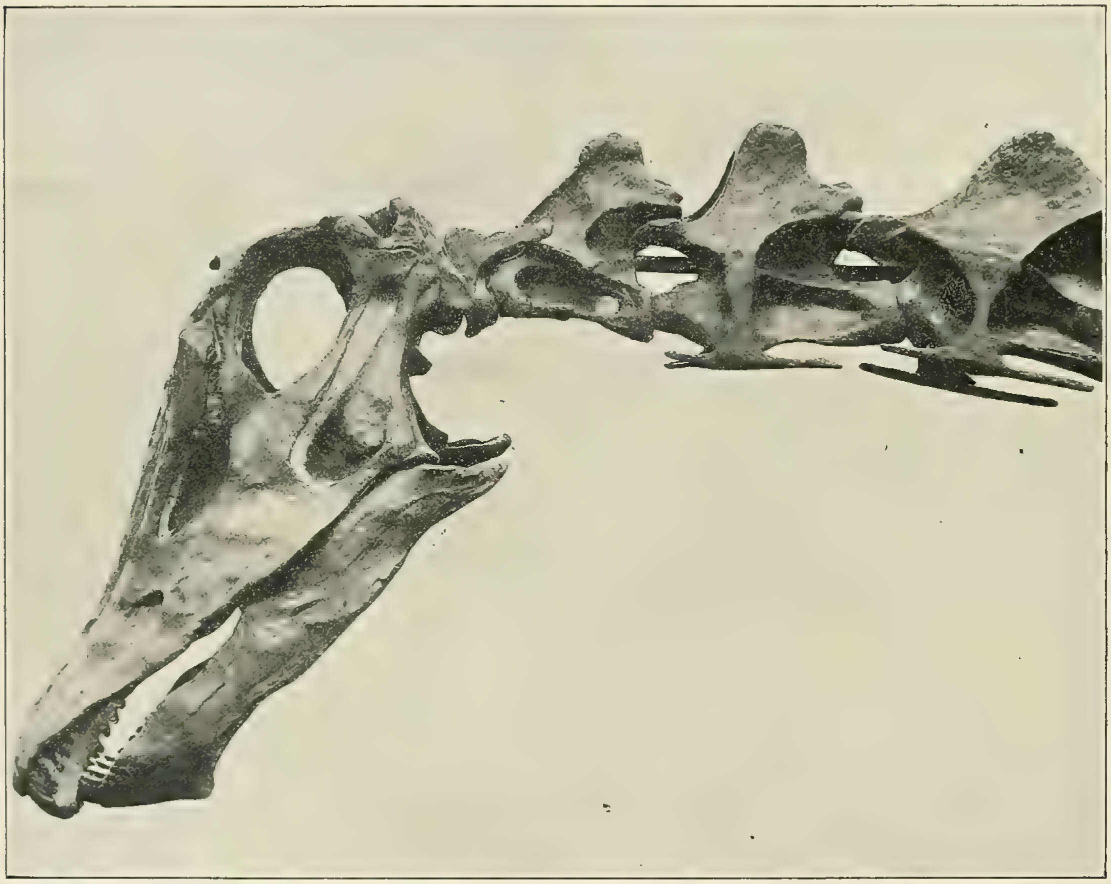


Fig. 1. Skull and anterior cervical vertebræ of *Diplodocus Carnegiei* Hatcher, as placed in the restoration at the British Museum (Natural History).

it, the front being much elevated, as in the ruminant mammals." When it became the duty of the writer to endeavor to assign the skull a position in the restoration in connection with the atlas and the axis, he was at once confronted by the fact that to place the skull with its longer axis in a line parallel with that of the cervical vertebræ was a mechanical and anatomical impossibility. The foregoing remarks of Professor Marsh had been overlooked by him at the moment, or they would have led him to a speedy solution of the difficulty. A careful study of the atlas, the axis, and the skull led him and his assistant, Mr. Coggeshall, after repeated failures to satisfactorily place the skull in the position usual among reptiles, to the final conclusion that the skull of Diplodocus in life was adjusted to the cervical series of vertebræ in such a manner that its longer axis formed an obtuse angle with the axis of the anterior cervical vertebræ. The correctness of this decision, which was the only one which could be reached, we subsequently found to be adumbrated and confirmed by the remarks of Professor Marsh, quoted above. Professor Marsh, though not called upon to articulate a skeleton of the animal, had with keen insight already detected the exceptional character of the skull with which he was dealing.

The figure on page 228 shows the skull of *Diplodocus* in the position assigned to it in the recent restoration of the skeleton. The attitude given the animal in the restoration is that which it might be imagined to have assumed when reaching forward with its long neck in quest of food. The motive in adopting this pose for the restoration was to bring the skull and the vertebræ of the neck within the range of easy vision on the part of observers. It is the opinion of the writer that the ani-

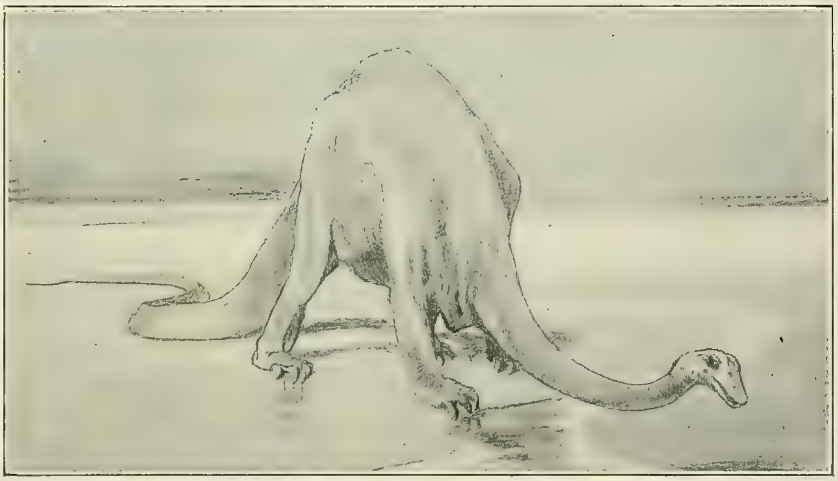


FIG. 2. Sketch by Miss Alice B. Woodward showing a supposable attitude of Diplodocus. (From the *Weekly Graphic*, London, May 13, 1905.)

mal in life may often, and, in fact usually, when at rest, have held its head in a position analogous to that in which the head is held by the struthious birds, or, as an acquaintance well expressed it in conversation, in "a cameloid position." The attitude referred to is hinted at in a sketch made by Miss Alice B. Woodward, the accomplished daughter of Dr. Henry Woodward, F.R.S. This sketch was published by the London *Weekly Graphic* in its issue of May 13, 1905, and is herewith reproduced by permission of the editors of that publication.

Further anatomical confirmation of the correctness of the position of the skull given in the restoration is afforded by the study of the inferior surfaces of the atlas and the axis when they are brought into apposition and articulated. It will then be observed that their under sides form a gently arching surface. To attempt to bring the atlas and the axis into a position which would enable the longer axis of the skull to be placed in a direct line with the cervical vertebræ and to place these vertebræ in a line with their inferior faces set absolutely horizontally involves the dislocation of the neck.

THE BONES OF THE SKULL.

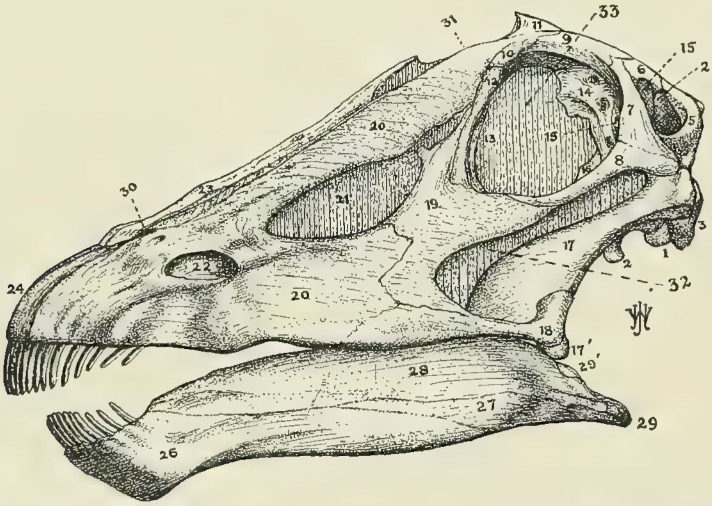


FIG. 3.—Side view of the skull of Diplodocus. 1, Occipital condyle; 2, basioccipital process; 3, end of left paroccipital process; 4, tip of posterior process of supraoccipital; 5, squamosal; 6, parietal; 7, postfrontal; 8, postorbital; 9, frontal; 10, prefrontal; 11, nasal; 12, supraorbital; 13, lachrymal; 14, orbitosphenoid; 15, alisphenoid; 16, presphenoid; 17, quadrate; 17′, hook-like lower end of quadrate; 18, quadratojugal; 19, jugal; 20, maxillary; 21, preorbital vacuity; 22, mesial foramen; 23, posterior processes of premaxillaries (according to Marsh); 24, premaxillaries; 25, supratemporal fossa; 26, dentary; 27, angular; 28, surangular; 29, articular; 29′, process of articular overlapping surangular; 30, foramen at posterior extremity of premaxillaries; 31, nasal opening (according to Marsh); 32, infratemporal vacuity; 33, orbital vacuity. (Figure one tenth natural size.)

The Basioccipital.—The basioccipital is terminated posteriorly by the occipital condyle, which, as has been pointed out by Professor Marsh, is "hemispherical, slightly subtrilobate in outline." The condyle is missing in Marsh's specimen No. 1922 (U. S. N. M., No. 2673) and he evidently based his description on specimen No. 1921 (U. S. N. M., No. 2672). The lower side of the bone in advance of the condyle is deeply concave longitudinally and convex transversely, throwing forward and downward a broad hypapophysis, which is divided into two portions, or basioccipital processes, at its anterior extremity. These processes point downward and backward. (See Figs. 3–5.) The body of the bone articulates by rough sutural surfaces with the basisphenoid, and the exoccipitals.

The Exoccipitals (Figs. 4–6, and 10). — The exoccipitals are broadly and strongly developed. Their inner margins, which are concave below, form the sides and the top of the foramen magnum in such a way as to show no trace of a suture in all specimens which the writer has examined. They send outward strong paroccipital processes, which are expanded above near their origin and again at their extremities. A sinus is thus developed upon the upper margin of the processes, and this forms the lower margin of the posttemporal fossa located between the paroccipitals and the squamosals, which by Professor Marsh was styled the "posterior fossa." The paroccipital processes articulate on the anterior surface of their outer

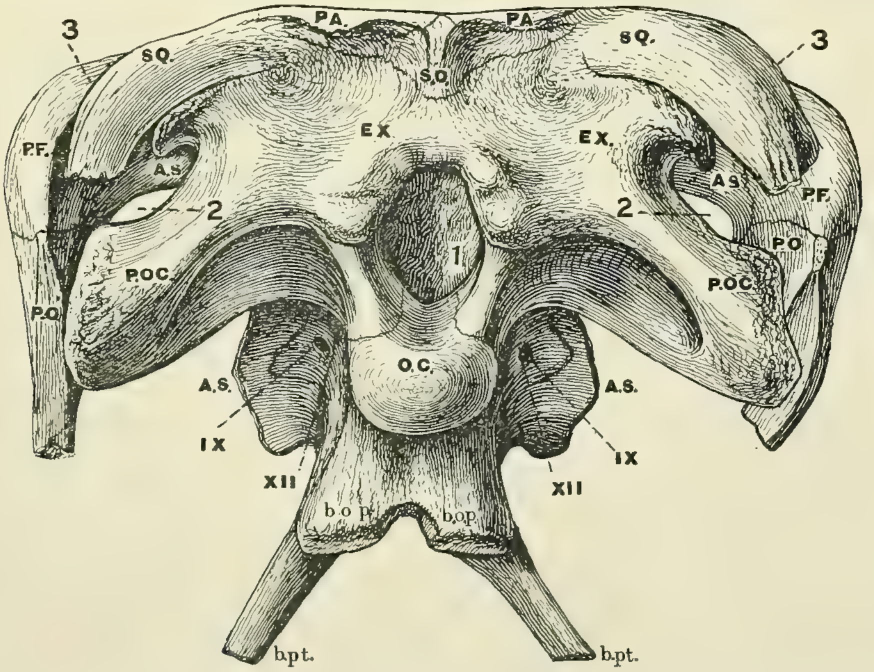


FIG. 4. Posterior view of back of skull of Diplodocus (No. $\frac{662}{22}$ Car. Mus. Cat. Vert. Fossils, one half natural size). *O.C.*, occipital condyle; *EX.*, exoccipitals; *S.O.*, supraoccipital; *PA.*, parietals; *SQ.*, squamosals; *P.F.*, postfrontals; *P.O.*, postorbitals; *AS.*, alisphenoids; *P.OC.*, paroccipital processes of exoccipitals; *b.o.p.*, basioccipital processes; *b.pt.*, basipterygoid processes; 1, foramen magnum; 2, posttemporal fossæ; 3, supratemporal fossæ; *IX.*, glossopharyngeal foramina; *XII.*, condyloid foramina.

extremities with the quadrate bones. Their ends project slightly beyond the quadrates, and the posterior and marginal surfaces reveal provision for strong muscular attachments. They articulate below with the basioccipital and above this on either side by a wing-like process with the alisphenoid, the lower portion of the wing of which meets and overlaps the wing of the exoccipital. On either side of the supraoccipital they articulate with the parietals, and beyond these touch the squamosals along the proximal portions of the inferior margins of the latter bones. In front on either side they articulate with the alisphenoids.

The Supraoccipital (Figs. 3, 4, and 6). — The supraoccipital is a comparatively small bone, rudely defined as quadrilateral in outline viewed from behind, which is wedged in between the exoccipitals and the parietals. Its posterior surface is produced as a strong process at the middle of the occipital crest for the attachment of the nuchal ligament. Its upper anterior portion in specimen $\frac{662}{22}$ (Carnegie Museum Catalogue) appears to advance for a short distance on the median line between the parietals, and is more strongly advanced in specimen No. 694 (Cat. Am. Mus. Nat. Hist.). (See Plate XXVII., Fig. 2.) On either side of this point in the specimens which the writer has examined it appears to be wedged in underneath the parietals, articulating with them by irregular rugose surfaces.

The Parietals (Figs. 3–6). — The parietals are small bones placed one on each side of the occipital crest, their outer surfaces constituting the lateral portions of this crest. They articulate posteriorly with the supraoccipital near the median line of the skull and beyond this on either side with the exoccipitals. At their outer extremities they articulate with the squamosals, the upper edge of the alisphenoids, and the postfrontals. (See Fig. 5.) In front they articulate with the frontals. Concerning their relation to the pineal foramen the writer will have some observations to make elsewhere. (See p. 243.)

The Squamosals (Figs. 3–6 and 8–9.) — The squamosals are hook-shaped bones curving outwardly and downwardly, forming with the upper antero-external portions of the exoccipitals the posterior upper wall of the supratemporal fossa, which is relatively small, and, as Professor Marsh has described it, "oval in outline, and directed upward and outward." The squamosals articulate on the inner portions of their inferior margins with the paroccipital processes of the exoccipitals. The outer portion of their inferior margins is free for about half the length of the bone forming the upper margin of the posttemporal fossa which Professor Marsh[3] in the case of the skull of his so-called *Atlantosaurus* denominates "the posterior fossa," and which at its upper end is bifid, as in *Atlantosaurus*, owing to the projection into it of an upper enlargement of the paroccipital process which assumes the form of a smaller lateral blunt process directed outward and downward. The squamosals are thin at their lower curving ends, where they articulate with the inner surface of the quadrates, which at their upper end are wedged in between the paroccipitals and the postorbitals.

---

[3] Dinosaurs of North America, Pl. XV., Fig. 1.

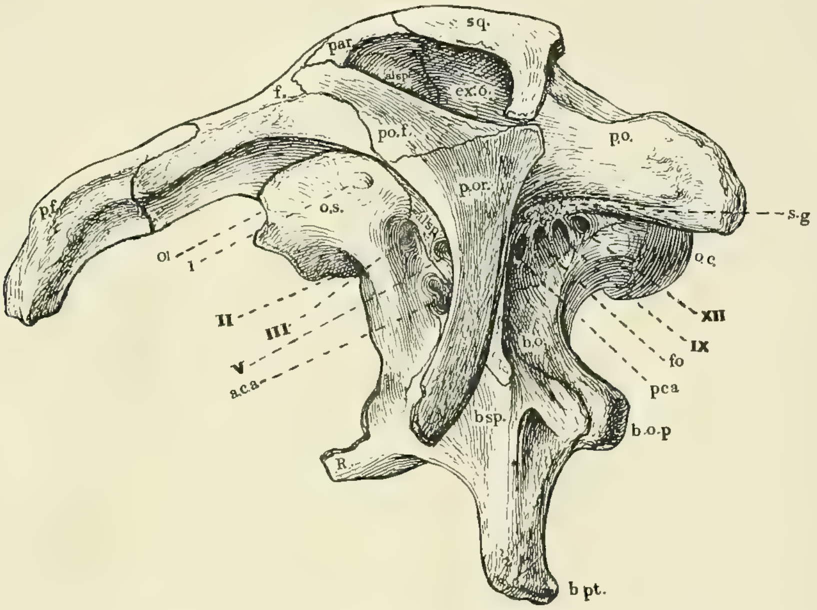


FIG. 5. Lateral view of the posterior portion of the skull of Diplodocus ($\frac{662}{22}$, Car. Mus. Cat. Vert. Fossils, one half natural size). *o.c.*, occipital condyle; *ex.o.*, exoccipital; *p.o.*, paroccipital process of exoccipital; *sq.*, squamosal; *par.*, parietal; *po.f.*, postfrontal; *f.* frontal; *p.f.*, prefrontal; *p.or.*, postorbital; *o.s.*, orbitosphenoid; *alsp.*, alisphenoid; *b o.*, basioccipital; *b.sp.*, basisphenoid; *b.o.p.*, basioccipital process; *b.pt.*, basipterygoid process; *R.*, presphenoid or rostral part of basisphenoid; *Ol.*, exit of olfactory nerves; *II.*, optic foramina; *III.*, oculomotor foramen; *V.*, trigeminal foramen; *IX.*, glossopharyngeal foramen; *XII.*, hypoglossal foramen; *a.c.a.*, foramen for anterior carotid artery; *p.c.a.*, foramen for posterior carotid artery; *fo.*, fenestra ovalis; *s.g.*, stapedial groove; 1, small foramen, possibly for vein.

The Frontals (Figs. 3, 5, 6, 8, and 10). — The frontals are paired, and united on the median line of the skull by a strongly toothed suture, extending in the specimen No. $\frac{662}{22}$ (Carnegie Museum Catalogue), from the point of union with the nasals to the parietals. The frontals over the orbital cavity are thick and heavy, measuring fully 1.5 cm. in thickness. They overlie the parietals posteriorly, and the nasals anteriorly, being bevelled in opposite directions on the lower side of the posterior and anterior margins for commissure with these bones. Each bone, viewed from above, sends out a short narrow anterior process at the point where they unite on the line of the median suture (Fig. 6, 4), and, another very long and broad process projecting forward, outward, and at its extremity downward (Fig 6, 5). This process is concavely bevelled below in front to receive the posterior margins of the nasals (Fig. 8, L. F. and R. F.) and grooved on its upper and outer side to receive the prefrontals (Fig. 6, P. F.). The orbital margin is horizontally concave (Fig. 6) and perpendicularly convex (Fig. 5). The posterior portions of the lateral margins of the frontals sweep downward to form the upper portion of the posterior wall of the orbital cavity, articulating with the alisphenoid, the postfrontals and the postorbitals. (See Fig. 8.) Along the posterior upper margin the frontals overlap the parietals, and articulate with the postorbitals on the upper margin of the process which the postorbitals send inwardly at the back of the orbital cavity. (See Fig. 8.)

The Postfrontals (Figs. 3–6, 8, and 9). — The postfrontals are small bones which overlap the frontals and the postorbitals, forming the upper portion of the anterior margin or wall of the supratemporal fossa and the upper posterior margin of the orbital arch. They articulate with the frontals and the postorbitals and posteriorly with the alisphenoid on the anterior wall of the supratemporal fossa. In the specimens studied by Professor Marsh he evidently regarded the postorbital bones as forming part of the postfrontals, and united the bones under the latter name. In his specimen (U. S. N. M., No. 2673) the distinctness of the postfrontals from the postorbitals is shown, and is conspicuously revealed in the specimen in the Carnegie Museum (No. $\frac{662}{22}$).

The Postorbitals (Figs. 3–6, 8, and 9). — The postorbitals assist in forming the posterior margin and a portion of the posterior and inferior inner walls of the orbital cavity. One portion of the bone extends as a somewhat sharp triangular process inwardly, being wedged between the posterior margin of the frontal bone and the upper portion of the wing of the alisphenoid which clasps it and supports it underneath. (See Fig. 8.) Above, this process is in part covered by the postfrontal where the latter bone unites with the external surface of the alisphenoid to form the anterior wall of the supratemporal vacuity. Externally where the postorbital articulates with the postfrontal the postorbital sends a process backward which articulates with the quadrate at the outer margin of the supratemporal fossa. The anterior part of the bone consists of a narrow process, triangular in section, running forward to a point where it articulates by an oblique suture with the upper posterior process of the jugal. The reëntering upper and lower surfaces of this process form respectively portions of the under surface of the posterior part of the orbital cavity and the upper surface of the posterior part of the infratemporal vacuity.

The Supraorbitals (Figs. 3 and 7). — The supraorbitals are long somewhat narrow bones forming very largely the anterior outer margin of the orbital cavity. They articulate above with the prefrontals and touch the uppermost posterior prolongation of the maxillary which borders the nasal opening; below they articulate with the superior process of the jugal, and along their posterior margin with the lachrymals. They might on account of their location be well styled preorbitals. In the specimen (~~U. S.~~ N. M., No 545), the bone is shown dislodged from its place and bent back across the matrix which fills the upper part of the orbital cavity. In the specimen (~~U. S.~~ N. M., No. 969), the bone is represented by some fragments (see Plate XXVI.), and in the specimen (U. S. N. M., No. 2672), it is shown just behind the antorbital vacuity. (See Plate XXIII.)

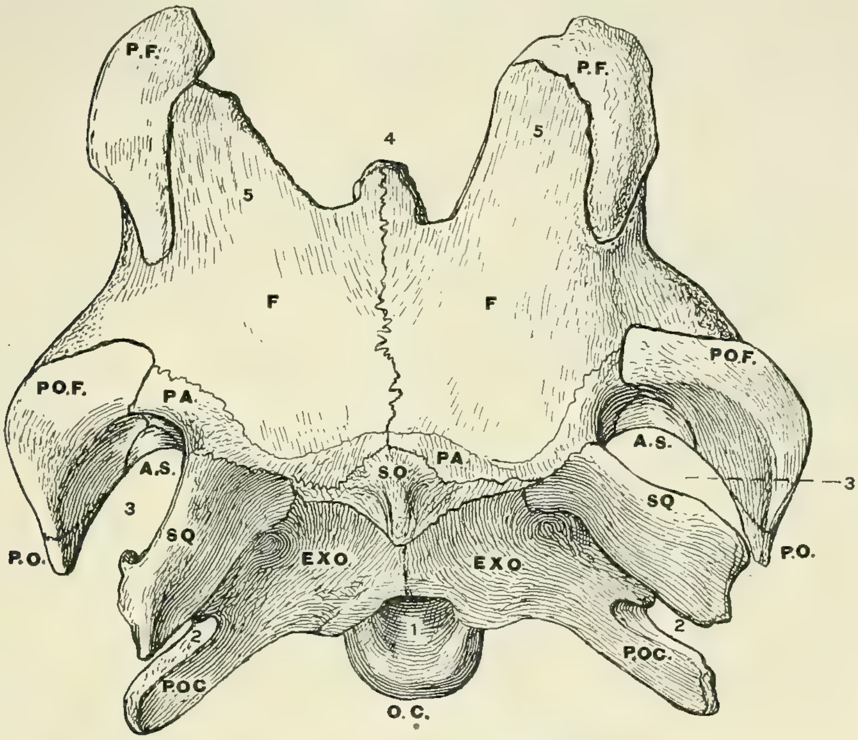


FIG. 6. Superior view of posterior portion of skull of Diplodocus (No. $\frac{662}{22}$, Car. Mus. Cat. Vert. Fossils, one half natural size). *O.C.*, occipital condyle; *EXO.*, exoccipitals; *P.OC.*, paroccipital processes of exoccipitals; *SQ.*, squamosals; *S.O.*, supraoccipital; *PA.*, parietals; *F.*, frontals; *PF.*, prefrontals; *PO.F.*, postfrontals; *P.O.*, postorbitals; *A.S.*, alisphenoids; 1, foramen magnum; 2, posttemporal fossæ; 3, supratemporal fossæ; 4, median anterior processes of the frontals; 5, lateral anterior processes of frontals.

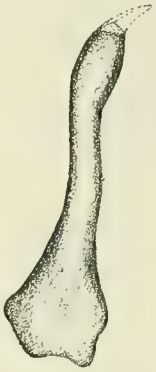


FIG. 7. Supraorbital. Sketch of the outline of the bone as shown in Marsh's type specimen (U. S. N. M., No. 2673). The upper end is broken off in this specimen. (One half natural size.)

The Lachrymals (Fig. 3).—The lachrymals are thin plates of bone articulating along the lower posterior margin of the supraorbitals and forming a portion of the lower anterior wall of the orbital cavity. The bone is found *in situ* in the type specimen of Professor Marsh (U. S. N. M., No. 2673). (See Plate XXIII.) It does not appear to exist in the specimen in New York (~~U. S. N.~~ M., No. 969).

The Basisphenoid (Figs. 5, 8, and 10).—The basisphenoid articulates posteriorly with the basioccipital and the exoccipitals and laterally with the alisphenoids and orbitosphenoids. The presphenoid or rostral portion is thin, occupying a vertical plane and forming a portion of the inner wall of the orbital cavity. The basisphenoid on either side sends downward and forward a remarkable long basipterygoid process and above these on either side sends out a flat lateral process which fuses with the lower wing-like processes of the exoccipitals and the alisphenoids at their point of conjugation.

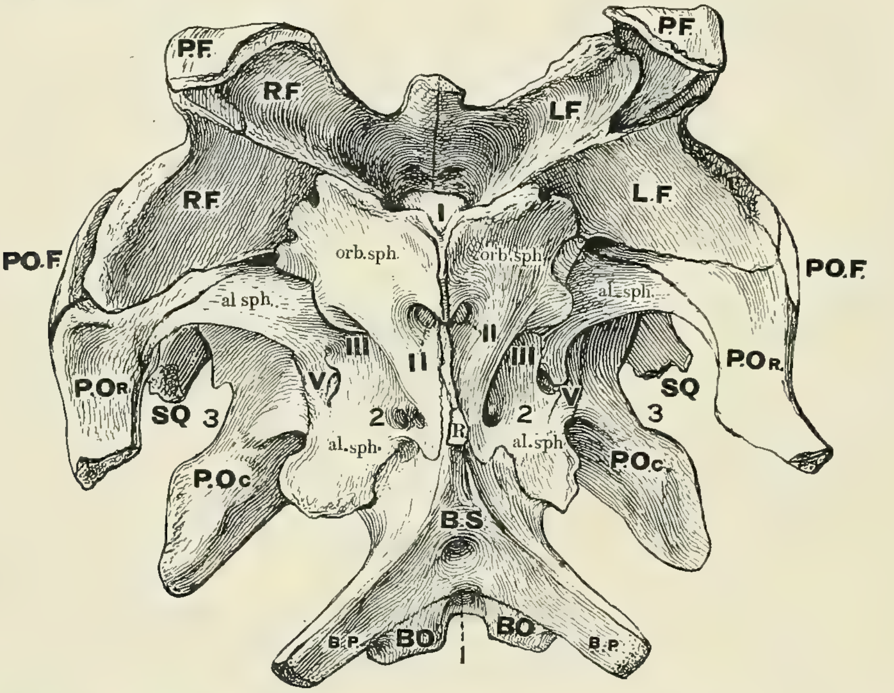


Fig. 8. Anterior view of posterior part of skull of Diplodocus (No. $\frac{662}{22}$, Car. Mus. Cat. Vert. Fossils, one half natural size). *P.F.*, prefrontals; *R.F.*, right frontal; *L.F.*, left frontal; *PO.F.*, postfrontals; *P.OR.*, postorbitals; *SQ.*, squamosals; *P.OC.*, paroccipital processes of exoccipitals; *BS.*, basisphenoid; *BO.*, basioccipital processes; *BP.*, basipterygoid processes; *R.*, rostral portion of basisphenoid; *orb.sph.*, orbitosphenoids; *al.sph.*, alisphenoids; *I.*, olfactory lobes; *II.*, optic foramina; *III.*, oculomotor foramina; *V.*, trigeminal foramina; 1, eustachian foramen; 2, foramina for anterior carotid arteries; 3, posttemporal fossæ.

The Alisphenoids (Figs. 3–6, 8, and 10). — The alisphenoids articulate dorsally with the frontals, postfrontals, postorbitals, parietals and exoccipitals; posterolaterally with the expanded wing of the exoccipitals where notches are formed on the line of conjugation for the exit of nerves, and anteriorly with the orbitosphenoids, at the line of union with which notches are likewise formed for the exit of nerves.

The Orbitosphenoids (Figs. 3, 5, 8, and 10). — The orbitosphenoids are paired meeting on the median line above the rostral prolongation of the basisphenoid. They articulate dorsally with the frontals and nasals, laterally with the alisphenoids, below with the basisphenoid. On the line of conjugation with each other notches are formed for the exit of nerves.

The Quadrate (Figs. 3 and 9 and Plate XXIII.). — The quadrate is a long bone articulating by its proximal extremity with the ends of the paroccipital processes of the exoccipitals, the squamosal, and the postorbital, uniting with these bones to form the outer margin of the supratemporal fossa. At its distal extremity it articulates for about five centimeters with the quadratojugal, under the posterior end of which it sends out a hook-like process for support. The quadrate at its lower extremity from about the middle broadens inwardly as a thin plate of bone, sending a process forward and downward to overlap the posterior ends of the pterygoid. This thin bony plate in part forms the inner lower wall of the infratemporal fossa.

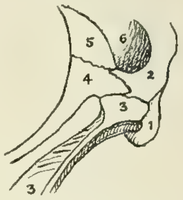


FIG. 9. Diagram showing the relation of the bones at the outer margin of the supratemporal fossa. 1, paroccipital process of exoccipitals; 2, squamosal; 3, quadrate; 4, postorbital; 5, postfrontal; 6, supratemporal fossa.

The Quadratojugal (Fig. 3 and Plates XXIII. and XXVI.).— The quadratojugal articulates in the manner already described with the quadrate by a flattened enlarged head, underlaid and hung in the hook-like extremity of the quadrate. The bone narrows below the infratemporal fossa into a comparatively narrow bar, and then widens to the line of articulation with the jugal and the maxillary. Just below this union along the outer margin of the upper jaw the bone expands and flares out horizontally. The manner of its articulation at both ends is best revealed by specimen No. 2673, U. S. N. M. (See Plate XXIII.) The specimen (A. M. N. H., No. 969) (see Plate XXVI.) has been restored in such a manner as to fail to show the true manner of articulation.

The Jugal (Fig. 3 and Plates XXIII. and XXVI.). — The jugal is a thin, very irregularly shaped bony plate which sends backward a long narrow process to articulate with the anterior process of the postorbital, with which process it unites to form the lower margin of the orbital cavity. Below it sends back another long narrow process to articulate with the quadratojugal. Between these two processes is a broad sinus forming the anterior margin of the infratemporal vacuity. Above, the jugal bone sends up a process which articulates with the preorbital at its lower end. This superior process further sends forth a small lateral process directed upward and forward, and projecting deeply into the posterior portion of the antorbital vacuity. The lower portion of the anterior margin of the jugal articulates by an irregularly curved line with the posterior border of the maxillary.

The Nasals (Fig. 3 and Plates XXIII. and XXIV.). — The nasal bones are paired bones somewhat semilunar in shape when seen from above. They are quite thin on their anterior margins, thick behind and are convexly bevelled posteriorly in order to articulate with the anterior margin of the frontal bone. They articulate also with the prefrontal bones along the anterior portion of their hind margins, the prefrontals being concavely bevelled at their extremities like the frontals, in order to receive them.

The Maxillary (Fig. 3 and Plates XXIII., XXIV. and XXVI.).—The maxillary is very largely developed and consists dorsally of a thin bony plate of irregular triangular outline forming the greater portion of the superior surface of the external walls of the facial region of the skull. On its ventral aspect it sends inwardly from its outer margin a broad lower plate, throwing out two long backward processes the innermost of which articulates, according to Professor Marsh, with the vomer, and the outermost of which articulates with the palatine, according to the same author.

The Premaxillaries (Fig. 3 and Plates XXIII., XXIV. and XXVI.). — The premaxillaries are paired subtriangular bones, occupying the triangular space in front of the skull between the maxillaries. They consist of an upper and lower bony plate. In all specimens examined by the writer the number of teeth in each premaxillary is four.

Premaxillary Processes (Fig. 3 and Plates XXIII., XXIV. and XXVI.).—Ranging backward from the premaxillaries, located between the maxillaries, are the two long slender bones, which Professor Marsh interprets as backward prolongations or processes of the premaxillaries, but which may be regarded as lateral ethmoids. These bones on the median line of the skull unite to form a raised ridge, which is higher in front than behind. At the anterior point of commissure the bones widen outwardly somewhat and terminate in blunt, outwardly obliquely truncated ends, which are raised above the level of the premaxillaries and maxillaries. There are at this point two moderately large foramina, one on either side, the purpose of which is yet to be determined, but which correspond more nearly in location to the nares as ordinarily found in the reptilia than any other openings in the skull.

Pterygoids, Palatine, and Vomer. — Professor Marsh's description of these bones was evidently based upon studies made by him after having taken the specimen (U. S. N. M., No. 2673) apart, so as to permit of a satisfactory examination of the roof of the mouth. At the time when the specimen was returned to the United States National Museum it was in separate pieces, and these have been reassembled so that it is now impossible to make a minute examination of the bones referred to, more particularly the palatine and the vomer. There is no reason to question the essential correctness of the brief descriptions and the figures given by Professor Marsh.

The Dentary (Fig. 3 and Plates XXIII. and XXVI.). — In the figure of the lower jaw given by Professor Marsh, "Dinosaurs of North America," Plate XXV., Fig. 1, he apparently represented the dentary as forming the superior border of the mandible for a considerable distance behind the last tooth of the lower series, and as forming the lower border of the mandible as far as a point a little back of the middle of the jaw. A critical examination of the skull (U. S. N. M., No. 2672) made by the writer in conference with Messrs. J. W. Gidley and C. W. Gilmore seems to show that the surangular extends forward almost to the point where the last teeth occur, and overlaps the dentary, while the dentary extends much further backward than is shown in Professor Marsh's figure. A comparison of Fig. 3 with Professor Marsh's figure reveals the difference in the interpretation given by the writer from that given by Professor Marsh in the drawing published by him.

The Surangular (Fig. 3 and Plates XXIII. and XXVI.).— The surangular externally overlaps the dentary from a point just back of the last tooth and forms the upper border of the jaw, extending externally almost to its posterior extremity. For about half of its posterior portion it articulates with the angular which is interposed between the posterior upper margin of the dentary and the lower posterior margin of the surangular. Internally the inner lamina of the surangular, beginning about three centimeters back of the symphysis, overlaps the dentary. Along its posterior inner surface it was apparently overlapped by the splenial which in the type specimen (U. S. N. M., No. 2672) seems to have been in great part broken away and lost, only some fragments of the lower posterior border remaining visible, wedged in between the surangular and the anterior internal prolongation of the articular.

The Angular (Fig. 3 and Plates XXIII. and XXVI.). — In the type specimen the angular is externally shown to be wedged in between the posterior margins of the dentary and the surangular, and extends backward to the extremity of the jaw. Internally it is shown to have had a heavy thickened middle portion lying back of the dentary and overlapped by an anterior prolongation of the articular.

The Articular (Fig. 3 and Plate XXIII.). — The articular forms the articulating surfaces of the jaw, overlapping the surangular at the posterior extremity by a well developed lateral process, and internally sending forth a long narrow prolongation.

The Coronoid. — In the specimen No. 2672 (U. S. N. M.) the coronoid like the splenial appears to be missing, the specimen being in this region somewhat defective.

The Teeth (Fig. 3 and Plates XXIII., XXIV., and XXVI.). — Professor Marsh pointed out the fact that the dentition of Diplodocus is weak. In all specimens of Diplodocus which have been examined there are four teeth in each premaxillary, as has already been pointed out. The number of teeth in the maxillaries and the dentary varies. In the specimen on which Professor Marsh founded his description there were nine teeth in the maxillaries and ten in the dentaries. In the specimen preserved in the American Museum of Natural History the number of teeth in the dentaries corresponds with the number given by Professor Marsh, but in the right maxillary in this specimen there are ten teeth while in the left maxillary there are eleven. The successional teeth are numerous, and nature provided the animal with the means of replacing a tooth almost as soon as it was lost. The arrangement of the teeth is rake-like, without distinct provision either for cutting or grinding, and suggests to the mind that they were employed for gathering soft succulent vegetation, which may have grown in masses upon the rocks of the shore. The feeding habits of the creature are, of course, unknown, but such teeth are apparently better adapted to raking and tearing off soft masses of clinging algæ than any forms of vegetable food which now exist in the waters of the world.

Openings in the Skull.

Larger Foramina. — The larger openings in the skull are the foramen magnum, the posttemporal fossæ, the supratemporal fossæ, the infratemporal vacuities, the orbital cavities, the narial opening, the preorbital vacuities, the large openings in the maxillaries, which I have designated as the mesial foramina of the maxillaries, and the foramina at the point of union of the premaxillaries and the long bones regarded by Professor Marsh as posterior processes of the premaxillaries.

The Foramen Magnum (Figs. 4 and 6 and Plates XXV., XXVI., and XXVII.). — The foramen magnum is bounded below by the basioccipital, and on either side and above by the exoccipitals. In specimen $\frac{662}{22}$, where there has been no crushing whatever in this region, the foramen is shown to be approximately ovoid in outline, with the longer axis perpendicular, the upper end decidedly narrower than the lower end of the opening. (See Fig. 4.)

The Posttemporal Fossæ (Figs. 4, 6, 8, and 10, and Plates XXV. and XXVI). — These are paired, one on either side of the exoccipitals. Each opening is bounded on its lower margin by the excavated margin of the paroccipital process of the exoccipital bones, and is bounded above by the lower margin of the squamosal. The upper end of the opening, when viewed from behind, is bifid, because of the intrusion into it of a short, blunt process which is sent forth downwardly and outwardly from the upper margin of the exoccipitals where they articulate with the squamosal. The lower extremity of the opening is closed by the proximal end of the quadrate.

The Supratemporal Fossæ (Figs. 3–6 and 10 and Plates XXIII.–XXVIII.). — The supratemporal fossa is oval in form, and is directed upward and outward. Its walls are formed behind, at the extreme upper inner margin, by the outer surface of the parietals for a short distance. The remainder of the posterior wall is formed by the forward surfaces of the exoccipitals and the squamosals. The anterior wall is formed at the extreme inner margin by the parietals, and the remainder of the anterior wall

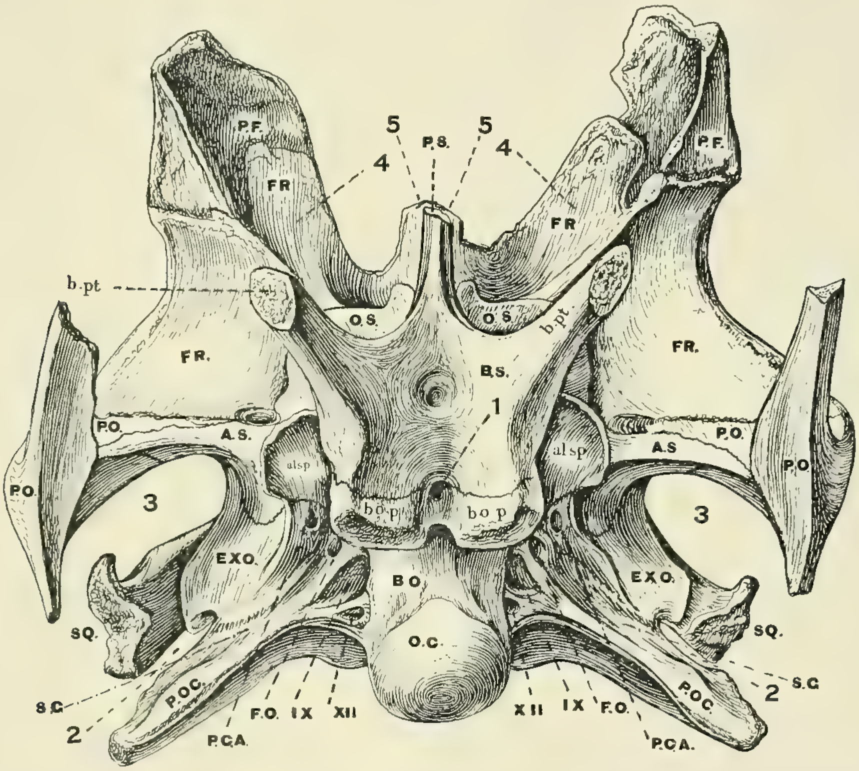


FIG. 10. Inferior view of posterior part of skull of Diplodocus (No. $\frac{662}{2}$, Car. Mus. Cat. Vert. Fossils, one half natural size). *O.C.*, occipital condyle; *BO.*, basioccipital; *P.OC.*, paroccipital processes of exoccipitals; *EXO.*, exoccipitals; *SQ.*, squamosals; *BS.*, basisphenoid; *AS.*, superior wing of alisphenoid; *alsp.*, inferior wing of alisphenoid; *P.O.*, postorbitals; *FR.*, frontals; *O S.*, orbitosphenoids; *P.S.*, presphenoid or rostral portion of basisphenoid; *P.F.*, prefrontal; *S.G.*, stapedial grooves; *P. C A.*, foramen for posterior carotid artery; *F.O.*, fenestra ovalis; *IX.*, glossopharyngeal foramen; *XII.*, hypoglossal foramen; *b.o.p.*, basioccipital processes; *b.pt.*, basipterygoid processes; 1, median eustachian foramen; 2, posttemporal fossæ; 3, supratemporal fossæ.

is formed by the posterior external surfaces of the postfrontals, the postorbitals, and the alisphenoid where the latter articulates between the postfrontal and the exoccipital. The internal surface of the upper end of the quadrate appears to form a small part of the inner margin of the supratemporal fossa above, but below enters into it to a larger extent.

The Infratemporal Fossæ (Fig. 3 and Plates XXIII. and XXVI.). — The infratemporal fossa is bounded above by the postorbital and the jugal, below by the quadrate and the quadratojugal.

The Orbital Cavities (Figs. 1, 3, 5, and 7–10 and Plates XXVIII. and XXVI.). — The orbital cavity is irregularly oval in form, with the longer axis lying in the direction of the longer axis of the skull. It is bounded above on its outer margin by the prefrontals, the frontals and the postfrontals; behind and below by the postorbitals, and below in front by the jugal. Its upper anterior margin is bounded by the supraorbital. The inner walls of the opening are formed by the nasals, the frontals, the orbitosphenoids and alisphenoids, and the process of the postorbital, which is thrust in between the frontal and the alisphenoid. The anterior portion of the wall is in part formed by the thin plate of the lachrymal, which articulates along the inner margin of the supratemporal.

The Narial Opening (Fig. 3). — The narial opening has been very accurately and correctly described and figured by Professor Marsh. It is, as he says, "very large, subcordate in outline, and is partially divided in front by the slender posterior processes of the premaxillaries. It is situated at the apex of the skull, between the orbits and very near the cavity for the olfactory lobes of the brain."

The Preorbital Vacuities (Fig. 3 and Plates XXIII., XXIV., and XXVI.). — The preorbital vacuity is phenomenally large, but by no means as large as it is represented in the restoration of the skull made by Mr. Hermann (A. M. N. H., No. 969) (see Plate XXVI.) and its outline is quite different, so far as can be determined from the specimens which are preserved in the United States National Museum. A comparison of the type skull, a photograph of which is given upon Plate XXIII. and of the accurate drawing published by Professor Marsh with the photograph of the skull restored by Mr. Hermann (a photograph of which is given upon Plate XXVI.) will show the great difference which exists. Unfortunately this portion of the skull employed by Mr. Hermann in making his restoration was missing, and the margins of this opening are wanting in the specimen, and in the restoration are wholly artificial.

The Mesial Foramen of the Maxillary (Fig. 3 and Plates XXIII., and XXIV.). — This opening, which does not occur, so far as is known, in any other genus of the Dinosauria, is about 5.5 cm. in length and about 3 cm. in width on its longest diameters. It is situated half way between the outer and inner margin of the maxillary bone and about midway between the posterior margin and the anterior extremity of the bone. It is very prominently and distinctly developed in both of the skulls, which are preserved in the collection of the United States National Museum. It has been, unfortunately, altogether ignored by Mr. Hermann in his restoration, and, as will be seen by reference to the photograph of this skull on Plate XXVI., it is not shown there. This foramen, which communicates with the interior of the nasal cavity, strongly suggests to the writer that it had a function supplementary to the function of the true narial opening.

The Foramina at the Junction of the Premaxillaries and the Posterior Processes of the Premaxillaries (Plate XXIV.). — At the point at which the premaxillaries touch the anterior extremities of the two long and narrow bones which Professor Marsh interprets as posterior prolongations of the premaxillaries (though these bones do not seem to the writer to be what Professor Marsh declares them to be) there is on either side of the anterior extremity of these bones a foramen approximately 3 centimeters in length and about .75 cm. in width. These two foramina extend with their longer axes parallel to the line of the symphysis of the two narrow bones, and the outer margin of each side is apparently formed by a narrow notch in the inner margin of the maxillary bone. These two foramina are very distinctly shown in Professor Marsh's type specimen (U. S. N. M., No. 2673). (See Plate XXIV.) They occupy a position which is relatively more nearly that which is held by the narial openings in many of the recent reptilia, and so far as the writer is able to judge from an examination of the skull, communicate with the narial cavity.

The Pineal or Parietal Foramen (Plate XXVIII.). — Professor Marsh, "Dinosaurs of North America," page 175, says: "On the median line, directly over the cerebral cavity of the brain, the type specimen of Diplodocus has also a fontanelle in the parietals. This, however, may be merely an individual peculiarity." On page 176 he says: "There is no true pineal foramen, but in the skull here figured, Plate XXV., there is the small unossified tract mentioned above. In one specimen of Morosaurus a similar opening has been observed, but in other Sauropoda the parietal bones even if thin are complete. The suture between the parietals and frontal bones is obliterated in the present skull, and the union is firm in all the specimens observed." A very careful study of the two specimens, which were jointly used by Professor Marsh while prosecuting his researches, as is evidenced by the drawings made at the time, some of which he used in his work upon the dinosaurs of North America, others of which he did not use, but which have been kindly placed at the disposal of the writer by the authorities of the United States National Museum, shows that in specimen No. 1921 (U. S. N. M. Catalogue, No. 2672) there is no evidence whatever of the existence of a pineal foramen. The opening in the top of the skull (see Plate XXIV.) is evidently due to artifical causes and has been produced either by accident, or by the use of an instrument. In the other specimen, No. 1922 (U. S. N. M. Catalogue, No. 2673), which is undoubtedly the specimen which Professor Marsh refers to as the "type," there is a protrusion upward of the matrix, with which the cerebral cavity had become filled, and the bone over this spot has largely disappeared, only a few flakes being adherent to the protruding mass of foreign matter. There is no depression at this point whatever, on the contrary there is an eminence. Both Mr. Hatcher and the writer were very skeptical as to the existence of a pineal or parietal foramen at this point, after we had carefully studied the original material upon which Professor Marsh based his description, and our skepticism was intensified by the study of the remarkably perfect posterior portion of the skull in our possession, to which reference has already been frequently made. In the latter specimen there is absolutely no evidence whatever of a pineal foramen. The two frontal bones unite by a suture which can be traced backward to the point where the frontals articulate with the parietals. (See Plate XXVIII., Fig. 1.) There are no Wormian bones and no evidence of the thinning out of the skull at this point. In the specimen which has been restored by Mr. Hermann of the American Museum of Natural History, he has represented a large and conspicuous foramen as existing at this point. Quite a considerable portion of the margin of this foramen is artificial. In another specimen belonging to the American Museum of Natural History, a photograph of which has been kindly sent to the writer by Professor Osborn, and which is reproduced on Plate XXVIII., Fig. 2, there is also shown an opening. A critical examination of this opening fails to disclose any true foraminal margins; on the contrary the edges examined microscopically show fractured surfaces. It is nevertheless quite possible that such an opening did exist in young and immature specimens and that it may have become closed up at a later period in the life of the individual.

The occurrence of such an opening, which is doubtful, but which, did it occur, must have disappeared with increasing maturity, does not seem to the writer to furnish any support to the theory of the existence, at all events in Diplodocus, of such an organ as the so-called "pineal eye."

Lesser Foramina of the Skull. — The beautifully preserved specimen (No. $\frac{662}{22}$, Carnegie Museum Catalogue of Vertebrate Fossils) shows with remarkable clearness the location of many of the smaller foramina of the posterior portion of the skull. These openings the writer has diligently compared with the foramina in the skulls of recent reptilia and with the foramina found in the skulls of extinct reptilia, so far as they are known and have been interpreted. He is under special obligations in this connection to Dr. C. W. Andrews of the British Museum for giving him an opportunity to compare the material in his possession with a portion of the skull of *Iguanodon bernissartensis* which is preserved in the British Museum and of which Dr. Andrews has published an interesting account.[4]

---

[4] *Annals & Mag. Nat. Hist.* (6th Ser.), Vol. XIX., p. 585.

Beginning at the point where the orbitosphenoids unite above we find a V-shaped fissure between the orbitosphenoids, which undoubtedly gave exit to the olfactory nerves. Just below this V-shaped opening the orbitosphenoids coössify for a short distance, and then by deep circular notches in their anterior margins (which notches are only separated by a short filament of bone on the median line) give exit to the second pair, or optic nerves. On the posterior margin of the orbitosphenoids, about their middle, where they coössify with the anterior surface of the alisphenoids, there are deep semicircular notches giving exit to the oculomotor and abducens nerves. Below the foramen just mentioned there are clustered three lesser foramina which evidently were intended to admit the anterior branches of the carotid artery and possibly also to give exit to veins. These foramina on the right side of the skull appear as three separate openings. On the left side of the skull the openings have become fused so as to form a somewhat large trilobate aperture.

Following the foramen which gives exit to the oculomotor nerves, at the point where the alisphenoids unite with the anterior surface of the exoccipitals and slightly below the level of the oculomotor foramen, there is a large foramen which is undoubtedly correctly determined as the trigeminal foramen. In outline, size, and location, it corresponds very closely to the trigeminal foramen in the skulls of recent reptilia.

In the lower margin of the exoccipital bone, somewhat above the line where it coössifies with the basioccipital, are four openings. The anterior opening which lies immediately behind the lower anterior wing of the exoccipital, which, as has been already said elsewhere, coössifies with the posterior wing of the alisphenoids, is a small foramen which very probably admitted on either side of the skull the posterior branches of the carotid artery. Immediately behind this is an opening which the writer interprets as the fenestra ovalis, leading away from which, along the lower margin of the paroccipital bone, is a groove which the writer interprets as the groove which held the stapes, which in the specimen in our possession is missing. Apparently no other location in the skull can be found save this for the exit of the auditory nerves, and a careful comparison of the skull with the skull of Sphenodon shows that this opening and the accompanying groove are closely analogous to the corresponding structures in the skull of the latter animal.[5] Succeeding this foramen is a foramen which the writer interprets as the exit for the glossopharyngeal nerves, and this foramen is in turn succeeded by a smaller foramen which passes through the lower margin of the exoccipital just at its point of union with the basioccipital and enters the posterior margin of the foramen magnum a little in advance of the occipital condyle. This foramen is most undoubtedly the foramen which gave exit to the hyoglossal nerve.

---

[5] Sphenodon has no external ear, agreeing in this respect with many other recent reptilia and ophidia. It is possible that Diplodocus had no external ear.

At the point where the basioccipital processes diverge anteriorly on the median line, just where union is effected between the basioccipital and basisphenoid bone, there is a deep foramen penetrating upward which the writer interprets to be, after the analogy of the crocodilian skull, the median eustachian foramen.

In addition to these foramina there are in the superior borders of the orbitosphenoid bones, where they unite with the frontals, small notches which may have given exit or entrance to blood vessels.

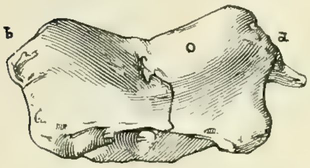
The attentive study of the foregoing account of the foramina of the cranium of Diplodocus reveals the fact that there is a close correspondence in the location of the various exits for the nerves of the brain between the skull under consideration and the skull of Iguanodon, a cast of the brain cavity of which was made by Professor Andrews and is beautifully delineated in the paper to which reference has been given. The brain of Diplodocus was however much more compressed antero-posteriorly. The cerebellum was less strongly developed, judging from a cast of the interior of the brain cavity of specimen No. 2673 (U. S. N. M.), which lies before the writer. The pituitary body in the brain of Diplodocus was not as strongly developed as in the brain of Iguanodon, though the impression of the interior cavity of the skull of Diplodocus before the writer is in many respects not as perfect as the impression secured by Professor Andrews, and it is therefore possible that the latter statement may hereafter require to be somewhat modified.

CERVICAL VERTEBRÆ.

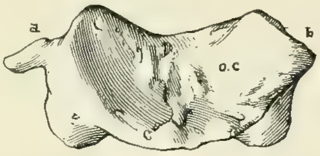
The Atlas.

Unfortunately, in all the material, which has been collected by the different expeditions sent out by the Carnegie Museum, no specimen of an atlas, which could unmistakably and positively be referred to Diplodocus, was found. The American Museum of Natural History was so fortunate as to secure an atlas with the skull (No. 969). The elements are disarticulated and somewhat crushed, nevertheless not so much so as to render it impossible to easily and correctly adjust the parts. The atlas figured by Professor Marsh ("Dinosaurs of North America," Plate XXVII. Figs. 1 and 2), and reproduced by Mr. Hatcher in his account (Memoirs of the Carnegie Museum, Vol. I., p. 19, Figs. 4 and 5), if the atlas of Diplodocus, is undoubtedly that of an older specimen, in which the different elements have become thoroughly fused and coössified. The elements of the atlas represented in the specimen belonging to the American Museum of Natural History are an intercentrum, two neural arches, and the odontoid process, figures of which, through the kindness of Dr. H. F. Osborn, I am permitted to give.

11.



12.



13.

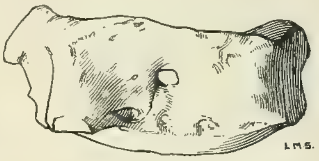


FIG. 11. Posterior view of intercentrum of atlas. *a*, right neurapophysial facet; *b*, left neurapophysial facet; *o*, odontoid facet. (One half natural size.)

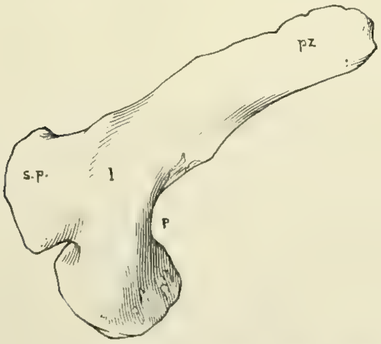
FIG. 12. Anterior view of intercentrum of atlas. *a*, right neuraphysial facet; *b*, left neuraphysial facet; *o.c.*, occipito-condylar facet. (One half natural size.)

FIG. 13. Inferior view of intercentrum of atlas. (One half natural size.)

The Intercentrum (Figs. 11–13). — The intercentrum is an irregularly oblong bone, flattened and somewhat concave on its lower side, sending forward a curving lip-like anterior projection along its lower anterior margin, and on either side of the hind margin throwing out two articular processes. The anterior surface is concave, adapted to accommodate the occipital condyle. The posterior surface is also concave, adapted to receive the odontoid process. On either side are broad facets for the right and left neural arches. The characteristic features of this bone are shown in the accompanying illustrations (Figs. 11, 12, and 13).

The Neural Arches (Figs. 14 and 15). — The neural arches are irregular bones, strongly concave inwardly and convex outwardly. They articulate with the intercentrum by means of a strongly-developed pedicle which flares out on all sides at the point where it coössifies with the intercentrum. In front the bone sends in-

14.



15.

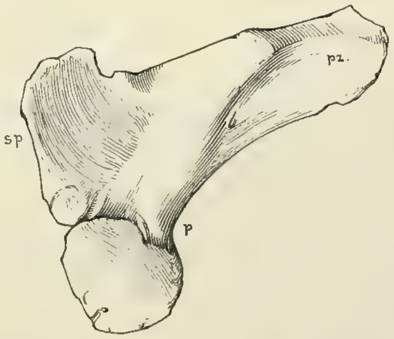


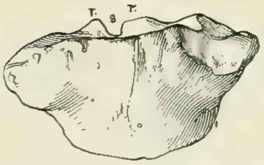
FIG. 14. External view of left neural arch of atlas. *p*, pedicle; *l*, lamina; *s.p.*, spinous process; *p.z.*, postzygapophysis. (One half natural size.)

FIG. 15. Internal view of the right neural arch of atlas. *p*, pedicle; *s.p.*, spinous process; *p.z.*, postzygapophysis. (One half natural size.)

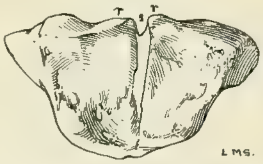
wardly and upwardly a process which with the corresponding process of the opposite arch forms the covering of the upper half of the neural canal. These processes do not, either in the specimen before us, or in the specimen figured by Professor Marsh, seem to have united to form a neural spine, and they were probably bound together by ligamentary attachments. The comparatively short lamina sends backward a greatly elongated postzygapophysial process, which in its anterior portion is excavated on the lower surface, and at its extremity on the lower surface is adapted to articulation with the prezygapophyses of the axis. In the specimen figured by Professor Marsh this process is represented as broken off, and Professor Marsh's figure, in which an attempt is made to supply the missing portion by a dotted line, does not give a correct idea as to its actual length.

The Odontoid Process (Figs. 16–19). — The odontoid process was not found with the axis described and figured by Mr. Hatcher. He says (Memoirs of the Carnegie Museum, Vol. I., p. 20): "Only the base of the odontoid process is preserved, but this indicates that it was of moderate length with a slightly concave superior surface." A careful examination seems to show that what was preserved of this specimen was the petrified cartilage intervening between the axis and the odontoid, to which some fragments of the odontoid were adherent, a partial coössification between the odontoid and the axis having taken place. In the specimen preserved in the American Museum of Natural History, figures of which are herewith given, it is plainly seen that this bone which is morphologically the centrum of the atlas, existed as a separate element of the cervix, as is always the case in the Chelonians, and exceptionally in the mammalia, even including man. The bone which is herewith figured and described has apparently sustained some slight injury on its upper surface, more particularly on the left hand side. It appears to the writer that a piece of the upper surface has been flaked off. The bone shows a distinct fracture, revealing the internal cellular structure on that side. Otherwise the bone shows well-preserved surfaces, and although slightly distorted by pressure, it is not so

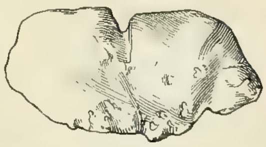
16.



17.



18.



19.

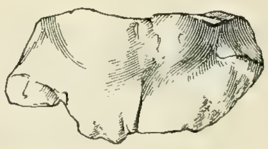


FIG. 16. Inferior view of Odontoid. *r.r.*, rugosities of upper posterior margin; *s.*, groove between rugosities. (One half natural size.)

FIG. 17. Superior view of Odontoid. *r.r.*, posterior rugosities; *s.*, groove through upper surface. (One half natural size.)

FIG. 18. Posterior view of Odontoid. (One half natural size.)

FIG. 19. Anterior view of Odontoid. (One half natural size.)

much distorted as to make it impossible to understand its relation to the atlas and axis. The bone may be described as having, roughly speaking, the form of a quarter of a sphere, the rounded surface fitting into the odontoid notch of the intercentrum of the atlas. This surface is not, however, perfectly rounded, but is somewhat constricted about the middle. The upper surface is approximately flat horizontally. Running through the middle is a small groove or sulcus, narrow in front and widening behind. The posterior surface is slightly concave, with two small rugosities projecting backwards, one on either side of the sulcus which has been described as running through the upper surface. The form of the bone is best understood by reference to the accompanying figures (Figs. 16–19). The superior surface of the odontoid of course formed, when in place, a portion of the lower wall of the spinal canal.

The Axis (Figs. 20–22). — The axis of specimen No. 84 (Carnegie Musum Catalogue of Vertebrate Fossils) has been very carefully described and has been well represented by Mr. Hatcher. He says in his description: "A short cervical rib without anterior process springs from the side of the centrum near its inferior margin and anterior extremity." A very careful reëxamination by the writer of the specimen upon which Mr. Hatcher's description was based leads him to think that the cervical rib on both sides has sustained injury, and that only a portion remains adherent to the centrum. Accompanying the elements of the atlas sent to the writer for study by the kindness of Professor Osborn are two bones, undoubtedly cervical ribs. They are both bones belonging on the right side of the centra. They are reported to have been found at the same place at which the atlas was found. The writer is inclined to think that the larger of these two bones (Fig. 20), was probably the rib of the atlas and indeed it requires but little effort to see that it might very well have served such a function, and that the smaller bone (Fig. 21) was the

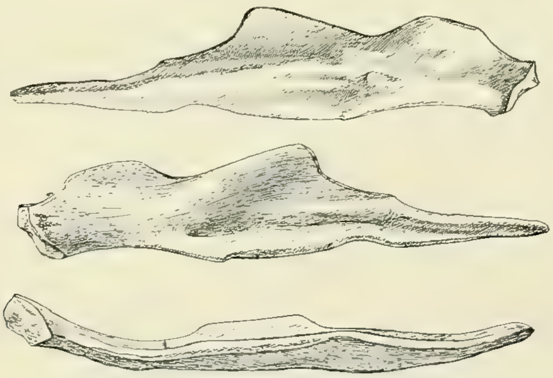


Fig. 20. Supposed rib of the atlas of Diplodocus preserved in the American Museum of Natural History. The upper figure is an external view of the rib, the middle figure is an internal view, the lower figure is an inferior view.

rib of the axis. Were the stump of the rib which remains attached to the axis in the Carnegie Museum, and which Mr. Hatcher has figured, removed, this smaller

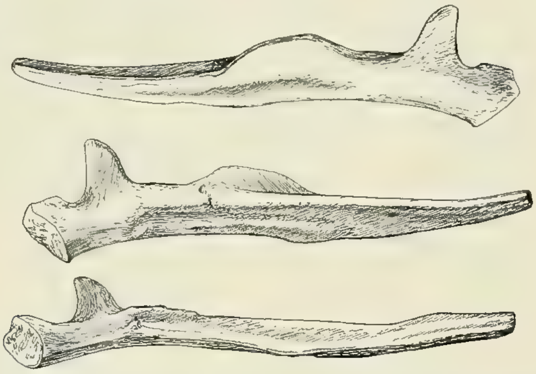


FIG. 21. Supposed rib of the axis of Diplodocus preserved in the American Museum of Natural History. The upper figure is an external view of the bone, the middle figure gives an internal view of the same bone, the lower figure is an inferior view.

rib might take its place and would undoubtedly articulate very neatly to the facet. In case the view entertained by the writer is correct, the form of the atlas and the axis with their attached ribs would be as given in the accompanying sketch (Fig. 22) rather than as given in the figure which has been published by Mr. Hatcher. Such a location of these parts has in its favor the analogy of the crocodilian skeleton.

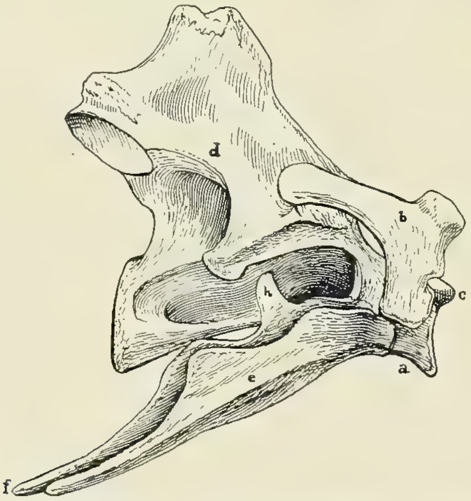


FIG. 22. Sketch of the manner in which the two cervical ribs preserved in the American Museum of Natural History may be supposed to have functioned in connection with the atlas and the axis. *a*, atlas; *b*, neural arch of atlas; *c*, odontoid process; *d*, axis; *e*, rib of atlas; *f*, rib of axis; *h*, anterior process of rib of axis.

The Cervical Vertebræ after the Axis. — Professor Marsh was undoubtedly in error in figuring as the cervical vertebra of Diplodocus the bone, an illustration of which is given in "Dinosaurs of North America," Plate XXVI., Fig. 3, and Plate XXVII.,

Fig. 3. This bone, the original of which was critically examined both by Mr. Hatcher and by the writer, is undoubtedly one of the cervical vertebræ of a Brontosaurus and not of a Diplodocus. The bones which were obtained by Professor Marsh in many cases came from what we are in the habit of calling "general quarries," that is, from deposits in which the bones of a number of individuals, sometimes representing different genera, are found commingled. The recovery by the Carnegie Museum in 1899 of the entire series of the cervical vertebræ of Diplodocus, most of them articulated and in the position held in the living animal has made the whole subject clear and any one at all familiar with the matter may easily verify for himself the correctness of the statement that Professor Marsh was in error in this particular instance. The fact that Professor Marsh had attributed one of the cervical vertebræ of Brontosaurus to Diplodocus had not been detected by Mr. Hatcher at the time that he prepared his first Memoir upon Diplodocus, but in Vol. II. of the Memoirs of the Carnegie Museum, p. 75, he points out the error into which Professor Marsh had fallen and calls attention to the fact that the comparison he made on p. 56 of his Memoir, between the cervical vertebræ of *Diplodocus carnegiei* and the cervical vertebræ attributed by Professor Marsh to *Diplodocus longus* is without value.

The cervical vertebræ belonging to the series after the axis have been so thoroughly and accurately described by Mr. Hatcher that it would be a work of supererogation for the writer to say anything in addition to what he has already so well said.

THE DORSAL VERTEBRÆ.

In a paper published by the writer in *Science*, N. S., Vol. XI., p. 816, it was stated that the number of dorsals ascertained to have belonged to specimen No. 84 (Carnegie Museum Catalogue of Vertebrate Fossils) was ten. At the time that this paper was written the vertebræ which are coössified and united with the ilia had not yet been freed from the matrix, and the fact that the anterior vertebra belonging to the five which are coössified in the sacral region might, as has been pointed out by Mr. Hatcher, be reckoned as a modified dorsal rather than as a true sacral, had been overlooked. Mr. Hatcher makes the first of the bones coössified in the sacral region the eleventh dorsal. He has, however, very aptly pointed out (Memoirs of the Carnegie Museum, Vol. I., p. 30) that it is a matter of individual opinion as to whether this bone should be reckoned as a sacral or as a dorsal. This vertebra marks the transition from the dorsals to the sacrals, and, as has been pointed out by Mr. Hatcher, "functions as a sacral." The number of vertebræ in Diplodocus to be reckoned as belonging to the dorsal series depends altogether upon the view which is taken of the composition of the sacrum. If the vertebræ which coössify in the sacral region and support the ilia are regarded as the sacral bones, then there are but ten dorsals. If the anterior vertebra of the five in the sacral region is considered, as has been done by Mr. Hatcher and Professor Osborn, a modified dorsal, then there are eleven.

THE SACRAL VERTEBRÆ.

Professor Marsh ("Dinosaurs of North America," p. 182) says, "There are four vertebræ in the sacrum. On Plate XXVIII. he gives a figure of the lower side of the sacrum in which he shows but three vertebræ. Professor Osborn in his monograph states, as Professor Marsh stated in his text, that there are four sacral vertebræ, and reckons as these four the three figured by Marsh in his plate and the succeeding vertebra." Mr. Hatcher says:

"The sacrum in Diplodocus may be regarded as composed either of three, four, or five vertebræ, according to the individual conception as to which should be considered as sacral vertebræ. If the sacrals are made to include all those vertebræ, which, though formerly belonging to the posterior dorsals or anterior caudals, have laterally become so modified as to function as sacrals by affording support to the ilia, either by bearing true sacral ribs, or by the means of greatly expanded transverse processes, or by both of these methods, then the sacrum of Diplodocus must be considered as composed of five vertebræ."

The fact is that five of the vertebræ are firmly coössified by their centra in this region and unite in supporting the ilia. All five perform the functions of sacral vertebræ. It appears to the writer that probably the most correct view to take of the the matter would be to say that the three vertebræ intervening between the modified dorsal and the modified caudal vertebra are the true sacrals, and to reckon the anterior vertebra with the dorsal series and the posterior vertebra with the caudal series.

THE CAUDAL VERTEBRÆ.

Mr. Hatcher accepted Professor Osborn's interpretation of the sacrals, fixing their number at four and including in the sacral series the modified caudal to which reference has been made by the writer in the preceding paragraph. Mr. Hatcher and Professor Osborn begin the caudal series with the vertebra next succeeding the one which functions as a sacral. Professor Osborn estimated the number of caudals as thirty-seven. Mr. Hatcher in his Memoir stated that "This number will more than likely be increased through the addition of a number of rod-like posterior caudals now known to obtain in the tails of certain other Dinosaurs." The correctness of the prediction made by Mr. Hatcher was strikingly shown by the discoveries made in 1901 and 1903. Mr. W. H. Utterback succeeded in 1903 upon the Red

Fork of Powder River, in finding the tail of a Diplodocus with the caudal vertebræ articulated and succeeding each other in regular order from very near the extremity of the tail forward to a point considerably beyond its middle. The study of this series of caudals in connection with the three other specimens acquired by the Carnegie Museum reveals the fact that the number of vertebræ estimated by Professor Osborn falls far short of the true number. In making the restoration which has been placed in the British Museum we utilized the twelve anterior caudals belonging to specimen No. 84 (Carnegie Museum Catalogue of Vertebrate Fossils) which had been found articulated and in the position held in life. From the caudal vertebræ found in connection with specimen No. 94 (Carnegie Museum Catalogue of Vertebrate Fossils) we selected nineteen caudals corresponding to the caudals belonging to the very beautiful specimen in the American Museum of Natural History which are figured by Professor Osborn and which when placed in position showed normal relationships to the anterior caudals, the position of which was absolutely ascertained, as well as to each other. The caudal No. 32 was supplied from the material obtained by Mr. Utterback on the Red Fork of the Powder River, belonging to specimen No. 307 (Carnegie Museum Catalogue of Vertebrate Fossils). Caudals 33 to 36 inclusive were taken from specimen No. 94. Caudals 37 to 73 inclusive represent the series found articulated and in position by Mr. Utterback in 1903. (See Plate XXIX.)

We were induced to select the vertebræ used in the caudal series taken from specimen No. 94 (Carnegie Museum Catalogue of Vertebrate Fossils) because of the fact that the specimen from which they were taken, though slightly smaller than specimen No. 84, corresponded more nearly in size to that specimen than caudals belonging to the specimens which were subsequently found. Caudals from 37 to 73 inclusive represent a specimen, which, judging from other bones (not vertebræ), which were found in connection with its caudal series, was a decidedly smaller individual than specimen No. 84, and even smaller than specimen No. 94. The total length of the caudal series made up in the manner which has been described, although at the first glance calculated to fill the observer with astonishment, is very probably shorter than the entire series would have been, had the specimen No. 307 attained as large a size as the other specimens which were utilized. Furthermore, in spite of the enormous prolongation of the tail which is shown, it is positively ascertained that not all of the vertebræ belonging to the caudal series are represented in it. The last caudal in the series plainly shows an articulation at its posterior extremity for the attachment of another caudal, and there may have been several succeeding it.

To recapitulate, we have brought together and arranged in making our restoration seventy-three caudals, not reckoning in this number the first modified caudal, which forms part of the sacrum. The vertebræ from 1 to 12 inclusive pertained to specimen No. 84; from 13 to 31 inclusive and from 33 to 36 inclusive, to No. 94. Caudal 32 and caudals 37 to 73 inclusive belonged to specimen No. 307.

The long whip-like prolongation of the tail of Diplodocus, the exact function of which is not known and can only be surmised, recalls the enormous prolongation of the tail which is shown in some recent reptilia. The writer has examined the skeletons of a number of species of recent reptiles and finds that the number of caudal vertebræ in *Iguana tuberculata* is sixty, in *Brachylophus fasciatus* sixty-five, in *Polychrus marmoratus* seventy, and in *Varanus niloticus* from ninety-seven to one hundred.

A comparison of the bones obtained in connection with the specimen of *Cetiosaurus leedsi* Hulke, preserved in the British Museum, indicates that they correspond approximately to the caudal vertebræ 47 to 56, inclusive, in the skeleton of Diplodocus. The bones of Cetiosaurus are relatively shorter and stouter than the corresponding bones in Diplodocus, but these bones both in the case of Cetiosaurus and of Diplodocus are remarkable because of the fact that they articulate both in front and behind by convex, or almost conical surfaces, showing that the posterior extremity of the tail possessed the very largest degree of flexibility. I am indebted to the courtesy of Dr. Arthur Smith Woodward for permission to give illustrations herewith of these vertebræ in *Cetiosaurus leedsi* Hulke. Fig. 23 shows an outline drawing made by Miss Alice Woodward, and Fig. 24 is a reproduction of a photo-

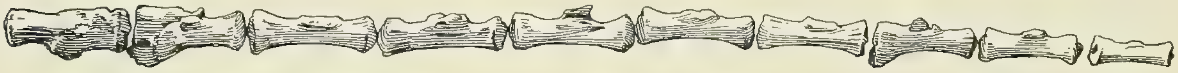


FIG. 23. Outline drawing of a series of posterior caudal vertebræ of *Cetiosaurus leedsi* Hulke. (One sixth nat. size.)

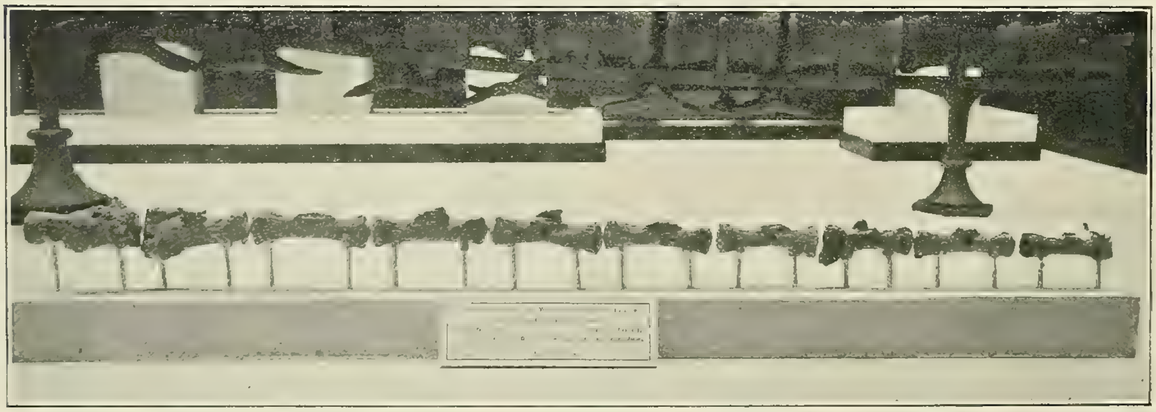


FIG. 24. Vertebræ of posterior part of the tail of *Cetiosaurus leedsi* Hulke, as exhibited in the British Museum (Natural History).

graph of the specimens as they are arranged for exhibition in the Gallery of Paleontology at South Kensington. Similar series of very slender rod-like caudal vertebræ have been recently found in connection with specimens of Brontosaurus.

That the enormously elongated, and at its extremity highly attenuated tail of these great reptiles was liable to injury, is shown by the caudal vertebræ of Diplodocus in the collections of the Carnegie Museum, as well as by the caudal vertebræ of *Cetiosaurus leedsi* preserved in the British Museum. In specimen No. 84 (Carnegie Museum Catalogue of Vertebrate Fossils) caudals 2 and 3 are coössified, as has been already pointed out by Mr. Hatcher in his Memoir, and this coössification appears to be pathological rather than normal. In specimen No. 94 caudals Nos. 20 and 21 are firmly coössified, as are also caudals Nos. 24 and 25. The coössified caudals Nos. 20 and 21 were described and figured as doubtfully Nos. 17 and 18 by Mr. Hatcher on page 36 of his Memoir. Maturer and more careful study has proved that they should be given the position which they now hold in the restored skeleton. The coössification in the case of both of these instances is evidently due to traumatic causes. An examination of the photograph of the rod-like caudals of *Cetiosaurus leedsi* (Fig. 24) shows plainly that several of these bones have sustained injury, as might easily happen by being crushed under the feet of other individuals, or when used possibly for purposes of defense in giving blows to the right and to the left.

Plate XXIX. represents the caudals from No. 37 to No. 73 inclusive as these were found in serial order by Mr. Utterback.

The Chevrons.

In the restoration of the skeleton represented by Mr. Hatcher in the Memoirs of the Carnegie Museum, Volume I., Plate XIII., the anterior chevrons are somewhat exaggerated in length. The chevrons had not been put into place at the time of Mr. Hatcher's death, and it fell to the writer to supervise this part of the work. The original drawing for Mr. Hatcher's plate was made by Mr. R. Weber, who based his drawings of the chevrons upon material which had not been experimentally assigned to positions in the skeleton. Mr. Hatcher's death compelled the writer to take up the work. The anterior chevrons used in making the reproduction were those found with our specimen No. 84, and these are shorter than those represented in the drawings made for Mr. Hatcher by Mr. Weber and accord, therefore, more nearly in proportion with physical requirements. Many of the chevrons after the first six are reproductions of those found and described by Professor Osborn in his paper on Diplodocus published in Volume I. of the American Museum of

Natural History, and we are greatly indebted to him for having kindly allowed us the use of this material. It is interesting to know that the chevrons of Cetiosaurus vary in form in much the same manner as those of Diplodocus, as has been shown by Professor A. Smith Woodward in his paper recently published in the Proceedings of the Zoölogical Society of London, 1905, Volume I., p. 239.

The Sternal Plates.

Among the puzzling elements of the skeleton of Diplodocus, as well as of other dinosaurs which have been discovered, are two bones to which Professor Marsh has given the name of "sternal plates." The location of these elements of the skeleton has occasioned a great deal of perplexity, and a careful examination of Professor Marsh's writings upon the subject shows very plainly that this distinguished authority was by no means certain as to either the location or the function which these large sesamoids hold in the skeleton. In his "Dinosaurs of North America," Plate XXII., Fig. 1, he represents the sternal plates of Brontosaurus with their thickened extremities directed upward and forward, and with their flattened and broadly expanded extremities directed downward and backward. On p. 179, Fig. 30, he represents the corresponding bones of Morosaurus in a reversed position. Both Mr. Hatcher and the writer discussed at great length and repeatedly the question as to the proper location of these elements, and finally reached the conclusion that the enlarged and thickened extremities of the bones, which manifestly display provision for the attachment of large masses of cartilaginous matter, should be located so as to point backward, while the thin margins should be directed upward and forward, thus making provision for the attachment for the ligamentary skeleton of the sternum, no portions of which have been found in a petrified form in any specimen which we have discovered, although in one specimen of Brontosaurus, which is described by Professor Marsh, there were found what he terms sternal ribs, which, manifestly, were more or less cartilaginous in their structure. It appeared to the writer, after a careful consideration of the subject, as altogether most probable, that the position which has been assigned these elements in the restoration is the correct one. There is no instance of record in all of the paleontological researches which have thus far been made, of the discovery of these bones in the exact position which they held in the life of the animal. They usually occur commingled with the anterior portions of the skeleton whenever this is found approximately *in situ*. In specimen No. 84 the sternal plates of the Diplodocus lay about the middle of the abdominal region, in a position to which they might easily have been brought as the bones of the decaying skeleton were shifted about by the agency of carnivorous animals or by the action of currents of water. That considerable shifting of this sort took place is shown by referring to the diagram of Quarry "C" (Memoirs Carnegie Museum, Vol. I., Plate I.) where it will be seen that the ischia had been shifted forward and were found lying in a position anterior even to that of the sternal plates.

The Supposed Clavicle.—In connection with specimen No. 84 (Carnegie Museum Catalogue of Vertebrate Fossils), there was found a bone, which was described by Mr. Hatcher on p. 41 of his Memoir upon Diplodocus. He expressed himself as strongly inclined to the opinion that it was a clavicle. In the Memoirs of the Carnegie Museum, Volume II., p. 74, he described a second specimen of a similar bone found in connection with skeleton No. 662 and gave figures. Mr. Hatcher adhered to the opinion that this bone might very well have functioned as a clavicle, though he also suggests that the bone may be regarded as an os penis. At the time that the restoration of the skeleton of Diplodocus was being set up I had with me a reproduction of the second specimen which belongs to skeleton No. 662, and Mr. Barlow, the skilful preparator in the Paleontological Laboratory of the British Museum,

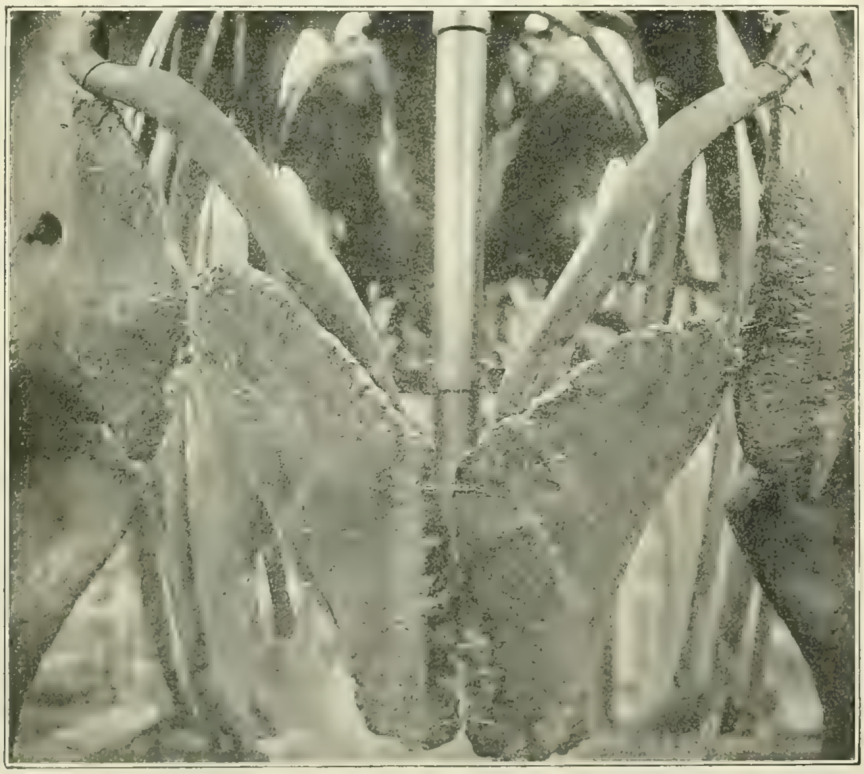


FIG. 25. Photograph of the two sternal plates and the supposed clavicles as provisionally and temporarily placed by the author in the pectoral region of the restored skeleton at the British Museum, May, 1905. The so-called clavicles have since been taken down and laid aside.

very kindly made for me a model, reversing the curvature so as to adapt this model for use upon the left side of the skeleton. The reproductions, one on the right side, the other on the left, were then placed in position by me, functioning as clavicles, the bifid extremity being located at the point of the symphysis of the coracoid with the scapula, at which point there is some evidence in all the specimens which we have found of provision for ligamentary or possibly osseous attachments. The broad, somewhat expanded distal extremities of the bones, as fitted into the skeleton, were found to adapt themselves very well to the back of the sternal plates, and the shallow groove running obliquely across the anterior surface of the bones seemed to adapt itself almost perfectly to the upper margin of the sternal plates as placed. Of all the supposable positions in which this bone might be put so as to function as a

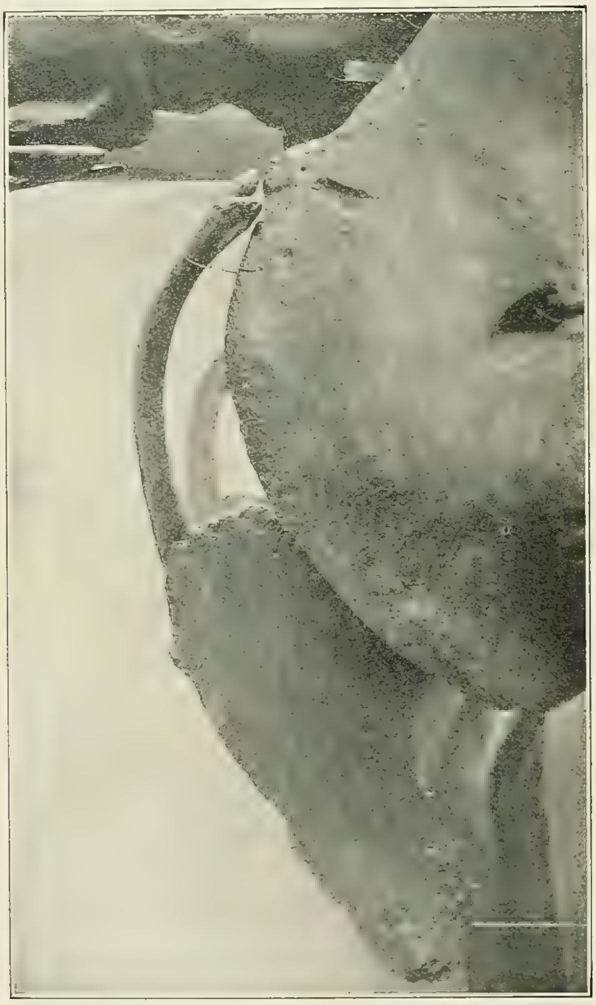


FIG. 26. Lateral view of the sternal plates and supposed clavicles as provisionally placed by the author in the pectoral region of the restored skeleton at the British Museum. The so-called clavicles were taken down and laid aside by the author.

clavicle, this appeared to the writer to be the most plausible, and the models of the bones were allowed to remain in this position for a short time. While in this position two photographs were taken, one from directly in front of the skeleton and the other at the side. These two photographs are herewith reproduced (Figs. 25 and 26), and serve to explain what the writer has said in the preceding sentences.

Against the location of the bones in the position tentatively assigned to them in the reproduction is *in the first place* the fact that the distal extremity of the supposed clavicle is brought into position behind the sternal plates. Such a location is very unusual, though not absolutely without an apparent parallel in other genera of the reptilia. In the Plesiosauria, as has been pointed out by Professor H. G. Seeley[5] and also by Dr. C. W. Andrews,[6] the clavicles are placed on the dorsal side of the scapular girdle. Figs. 27 and 28 represent the position of the clavicles in a specimen of *Cryptoclidus oxoniensis*, which is preserved in the British Museum. Fig. 27 furnishes a view from above of the clavicles lying in position upon the shallow-grooved surfaces in the scapula where they were found *in situ* when the specimen was discovered. I understand from Dr. A. Smith Woodward that there is no doubt

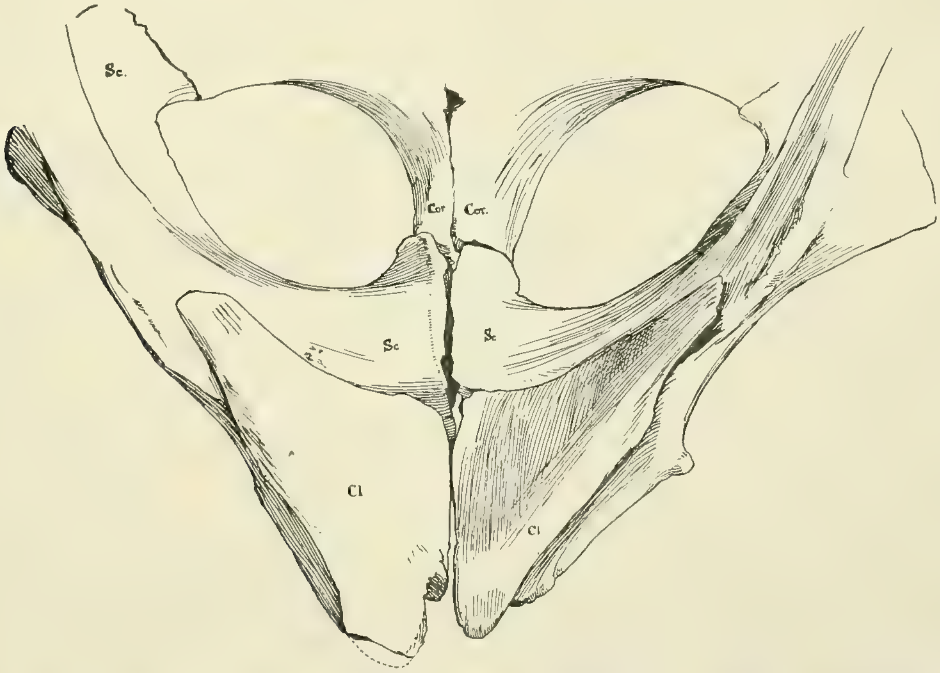


FIG. 27. Superior view of the pectoral girdle of *Cryptoclidus oxoniensis*. *Cl.*, clavicle; *Cor.*, coracoid; *Sc.*, scapula. (Drawn by Miss Alice B. Woodward.)

---

[5] "The Nature of the Shoulder Girdle and Clavicular Arch in Sauropterygia," by H. G. Seeley, F.R.S. *Proceedings of the Royal Society*, Vol. LI., pp. 119–151.

[6] "The Pectoral and Pelvic Girdles of Muræenosaurus plicatus," by C. W. Andrews. *Ann. and Mag. Nat. Hist.*, April, 1895, pp. 429–434.

that the bones in this specimen of *Cryptoclidus* are located in the position which they held when first found. Fig. 28 is a view of the scapular girdle of the same specimen viewed from directly in front and showing the clavicles lying on the dorsal surface of the scapula. To place the supposed clavicles of Diplodocus in the position shown above in Figs. 25 and 26 has therefore the analogy of the location of the clavicles in the skeleton of *Cryptoclidus* to support it.

In the second place, against the employment of these bones as clavicles is the fact that, so treated, their articulation with the margin of the scapula and the coracoid where the latter bones unite must be made by a bifid extremity. The writer, from an anatomical standpoint, does not contemplate such an articulation as this with satisfaction. It is without analogy in other forms to support it. He knows of no case among recent or extinct reptiles where the articulation of the clavicles with the scapular elements takes place by means of bifid extremities.

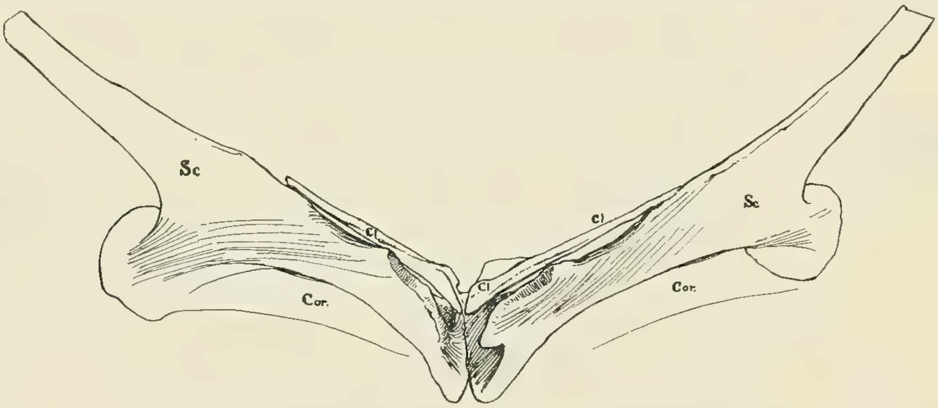


FIG. 28. Anterior view of the pectoral girdle of Cryptoclidus. *Cl.*, clavicle; *Cor.*, coracoid; *Sc.*, scapula. (Drawn by Miss Alice B. Woodward.)

Baron F. Nopsca, Jr., who occasionally called upon the writer while at work upon the restoration, has since caused a paper to be presented at a meeting of the Zoölogical Society of London which has been published (cf. *P. Z. S.*, London, 1905, Vol. II., Part I., p. 269). In this paper the Baron undertakes to break a lance in defence of the suggestion made by Mr. Hatcher, that this bone might possibly have had the function of an os penis. Against this view there is very much to be said. As Mr. Hatcher pointed out in Volume II. of the Memoirs of the Carnegie Museum, p. 74, "The marked asymmetry of the bone" offers a potent argument against the probability of this assumption. At the time that I was experimenting at South Kensington, in the endeavor to utilize these bones as clavicles, I had with me only a reproduction of the specimen which had been found in connection with skeleton No. 662, but since my return to the Carnegie Museum I have very carefully reexamined not only the specimen from No. 662, but also the specimen which was found with No. 84. I find that the two bones are, in spite of what Mr. Hatcher said, highly dissimilar, and it even appears that they may have functioned as bones of opposite sides of the skeleton. Their shafts are not cylindrical, but flattened on one side and convex on the other. They are not alike at either extremity. When placed side by side with the lines of their curves approximately parallel, it is at once seen that the broad flattened extremity of the bone recovered with skeleton No. 662 lies in a plane varying from that in which the corresponding portion of the bone found with skeleton No. 84 by an angle of at least 40°. (See Fig. 29.) If these bones are regarded as belonging to the male copulatory organ then it becomes plain that the position held by this organ in the two specimens must have been wholly different. Accepting for sake of argument the view that the flattened end of the bone represents the portion of the os penis which was located in ligamentary attachments, proceeding from the corpus fibrosum, with its plane placed vertically after the analogy of *Lutra* and other animals, then its distal extremity lay in nearly the same plane pointing downward, with the convex side of the shaft on the right, and the flattened side of the shaft on the left. Assigning to the specimen from No. 84 the same position, so far as its flattened, supposedly proximal end is concerned, its distal

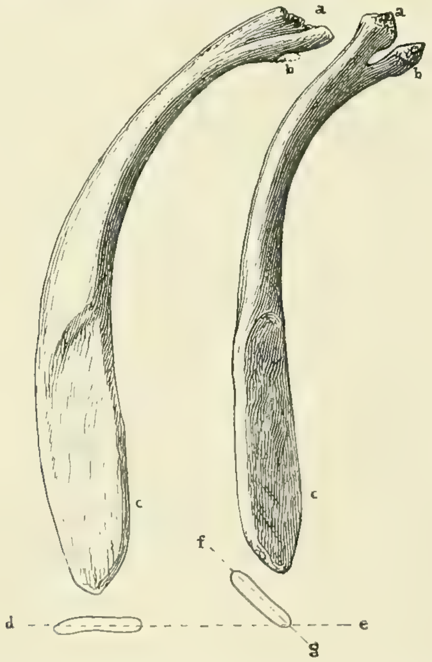


FIG. 29. The two supposed clavicles lying side by side with their curves approximately parallel. The figure on the left is that of the bone recovered with skeleton No. 662, that on the right is the bone recovered with skeleton No. 84. *a-b*, bifid extremities of bones; *c*, broad flattened ends of bones; *d-e*, direction assumed by flattened end of bone from No. 662; *f-g*, direction assumed by flattened end of bone from No. 84.

extremity must have pointed upward and strongly to the right. If, however, leaving the direction of the flattened ends of the bones out of sight, we place the two with the flattened sides of their shafts in one position, so that the shafts occupy the same relative position, then the bone from No. 662 points downward, while the bone from No. 84 points upward and strongly to the left. It is wholly inconceivable to the writer that such absolutely dissimilar arrangements should exist in the case of the penis bone of any animal. Sectional drawings of the shafts of these bones also show that they are very different from each other. (See Fig. 30.) The bone taken from skeleton No. 662 is very rib-like, the shaft having a flattened surface on one side and a convex surface on the other. The bone taken from skeleton No. 84 has the same flattening on one side and a convexity on the other, though not so strongly developed. The bifid extremity of the bone from No. 662 shows that a small portion of one of the branches has been broken off, but irrespective of this fracture the end does not agree with the bone from skeleton No. 84 either in the shape or direction of the surfaces of the bifurcating extremities. While Mr. Hatcher was inclined to the view that both bones represented specimens taken from the same side of the animal, it appears to the writer that they may very well be bones from opposite sides. Not only are these bones, therefore, asymmetrical, but they differ in a marked manner from each other to such an extent as to suggest that they did not occupy the same place in the skeleton, but were most probably from opposite sides.

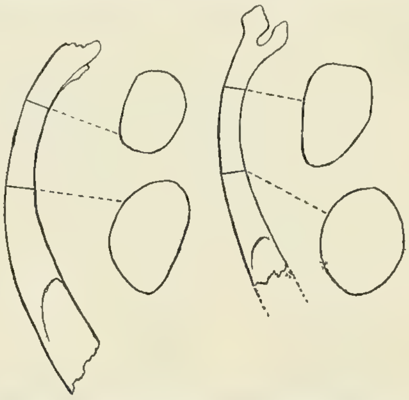


FIG. 30. Sections one third of natural size of shafts of supposed clavicles. The upper figures represent sections taken four and one half inches from the bifid end of the bone, the lower figures represent sections taken nine and one half inches from the same point. The outlines of the bones themselves are reduced much more than one third and are wholly diagrammatic. That on the left is from skeleton No. 662, that on the right from skeleton No. 84.

Finally, against the theory advanced with great hesitation and rejected by Mr. Hatcher, but which Baron Nopsca has undertaken to defend, that these bones might have functioned as ossa penis, is not only the fact of their asymmetry and the marked differences which exist in the two specimens, which are so great as to make it appear, that, wherever located in the skeleton, they must have held opposite, or, at least, very different positions, but the fact, that, so far as is known to the writer, there is no record in any museum, or in all of the literature of the subject, of the existence of an os penis among any of the reptilia, living or extinct, whereas clavicles are found in many reptilian genera. The similarity of these bones to the os penis of *Lutra*, which is pointed out by Baron Nopsca, is curious, but entirely fails to carry conviction with it to my mind, and more particularly since I have carefully reëxamined the original specimens which are in my custody. The fact of the bifidity of the penis of *Struthio*, which is pointed out by Baron Nopsca, does not appear to the writer to possess great weight. The tracing of resemblances between the struthious birds and the dinosauria appears to the writer, as he knows it does to others, to be in danger of being greatly overdone. Bifidity in the penis is characteristic of the organ in many widely different groups of animals.

There is another thought or suggestion which has presented itself to the mind of the writer during his studies, namely, that these bones may possibly have been sternal ribs connected in some way by strong cartilaginous or ligamentary attachments with the roughened and thick ends of the sternal plates, or imbedded in cartilaginous or fibrous muscular tissues which do not exist in a fossil state in our specimens. In this connection reference may be made to the sternal ribs obtained with a skeleton of Brontosaurus, which Professor Marsh has figured in his work upon the Dinosaurs.[7] It is worthy of note that the length of the longest and most attenuated of these bones is almost identically that of the supposed clavicle described by Hatcher. It is furthermore inconceivable to the writer that there should have been no sternal ribs in Diplodocus. There must have existed a system of central supports for the lower part of the wall of the huge thoracic cavity.

The attempt to assign these bones to a position in which they may function as clavicles is not wholly satisfactory to the writer. To regard them as ossa penis is to the writer a far more thoroughly unsatisfactory hypothesis, as it was to his colleague, Mr. Hatcher, who first suggested it. The conclusions of my friend Baron Nopsca, reached in a labored argument based upon seven propositions, the first five of which bear only indirectly upon the subject, and the last two of which are positively incorrect, are in the judgment of the writer untenable. The true position of these bones is still in doubt, and having left the reproduction of them for a few days in the position to which I had tentatively and experimentally assigned them in the model of the skeleton, I removed them and turned them over to Dr. Arthur Smith Woodward, requesting him to keep them until with the progress of discovery we come to a point where we may be better able to tell what was the rôle which they actually played in the osseous system of Diplodocus.

---

[7] "Dinosaurs of North America," p. 171.

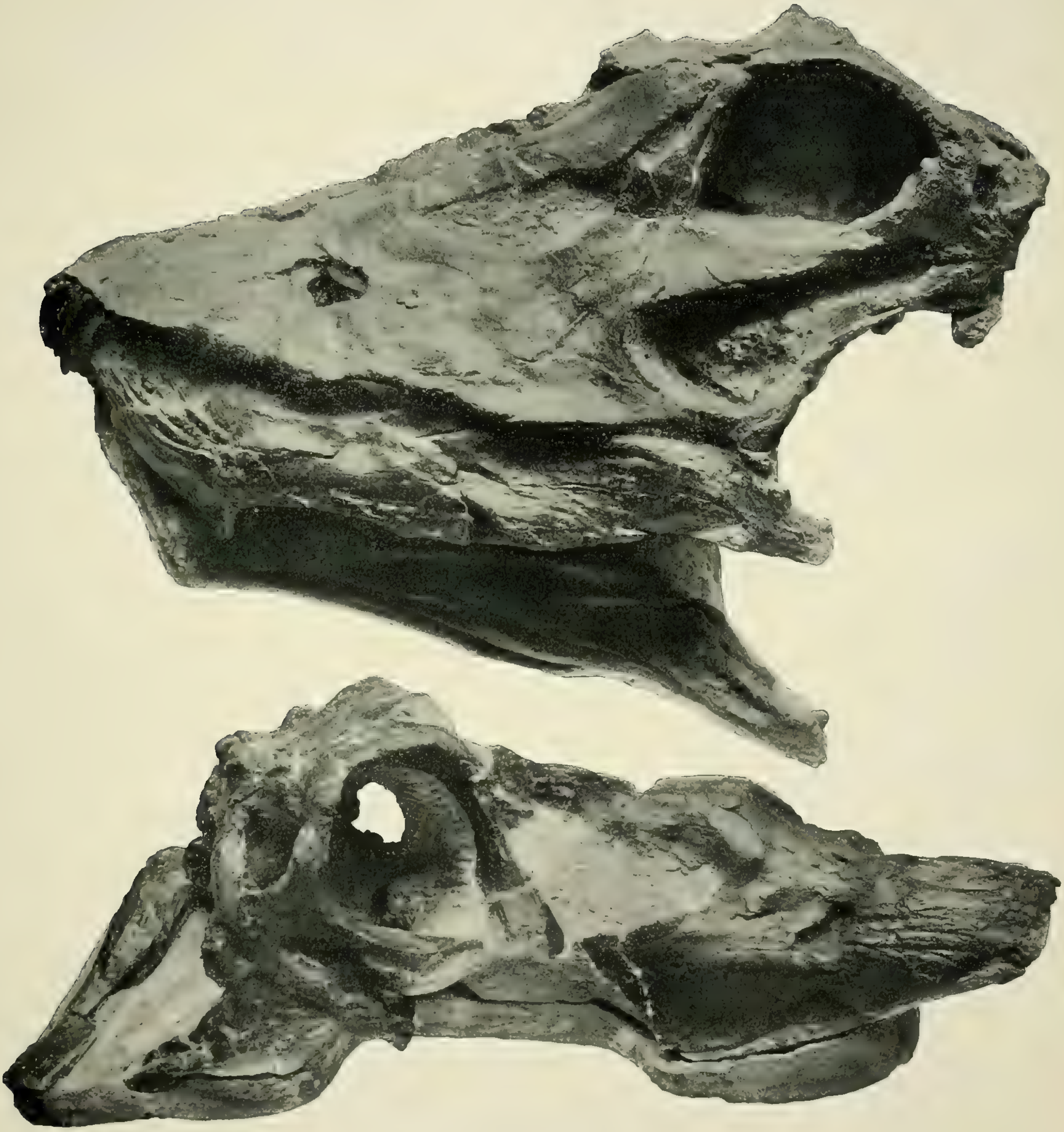
In concluding this brief paper upon the osteology of Diplodocus the writer cannot forbear making passing reference to the interest which was manifested by the public in the restoration, which was formally presented to the Trustees of the British Museum by Mr. Carnegie, on May 12, 1905. He is informed that the number of persons resorting to the Museum in South Kensington, after the announcement had been made that the restoration was on view, exceeded the attendance at the institution at any time since the building was first thrown open to the public. It happened that at the time of the presentation Parliament was in session, and it was exceedingly interesting, as well as amusing, to observe the manner in which the fancy of the knights of the quill and brush seized the work of the paleontologist to aid them in the field of political caricature. A score of amusing cartoons bearing upon the political events of the day, in which the Diplodocus was made to do service, appeared in the daily papers of England. In the field of commercial advertisement the great reptile has been used, and the writer has discovered a number of advertisements in which rude representations of the creature have been given, in order to attract the attention of the public to wares which are described below the cuts. Not only has the Diplodocus been pressed into service by the caricaturist and the advertising agent, but the modeler has employed its form for decorative purposes. "Diplodocus vases," bearing on their sides figures of the beast in high relief, have been placed upon the market in London by one of the best known firms engaged in the manufacture of majolica.

Thus the huge reptile, which a score of years ago was unknown, has become more or less familiar, although there remain a number of doubtful points as to its osteology to be solved by future study and research.

EXPLANATION OF PLATE XXIII.

The upper figure represents the left side of the skull which bears Professor Marsh's number 1922 (U. S. N. M., No. 2673). The mandible on the right side is dislocated and crushed down.

The lower figure represents the right side of the skull which bears Professor Marsh's number 1921 (U. S. N. M., No. 2672). The specimen is badly broken and crushed in part, but the occipital region is in part better preserved than is the case in the specimen represented in the upper figure. The drawings of the skull of Diplodocus published by Professor Marsh, as well as other drawings, which he caused to be made, but which he did not publish for reasons which are plain to the critical student, show that he utilized both of these skulls in preparing his descriptions and published figures.

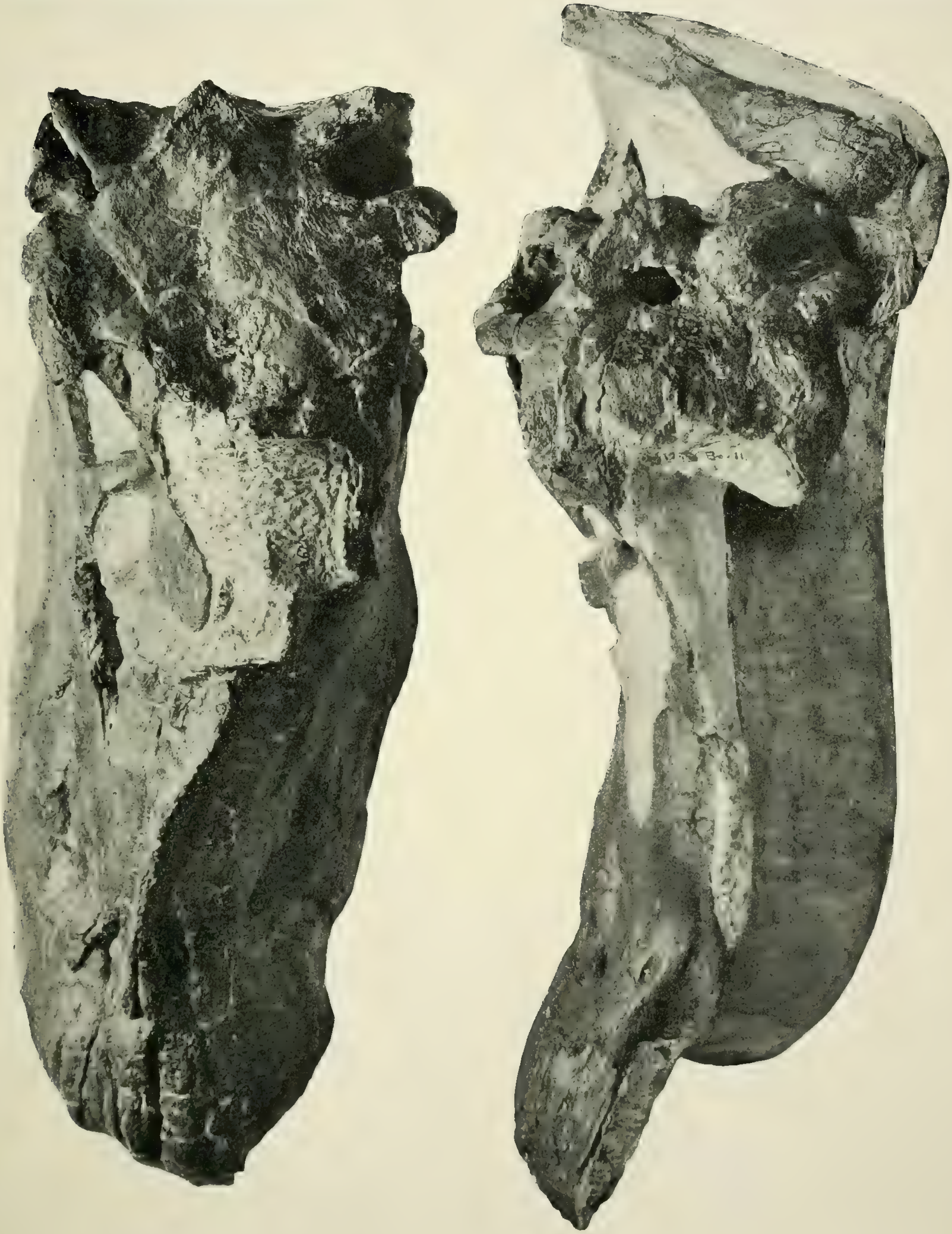


SIDE VIEW OF SKULLS OF *DIPLODOCUS LONGUS* MARSH, PRESERVED IN THE UNITED STATES NATIONAL MUSEUM.

EXPLANATION OF PLATE XXIV.

The figure on the left is a view from above of the skull of Diplodocus bearing Professor Marsh's No. 1922 (U. S. N. M., No. 2673). The photograph shows that the right side of the skull has been more exposed to crushing than the left.

The figure on the right is a view from above of the skull of Diplodocus bearing Professor Marsh's No. 1921 (U. S. N. M., No. 2672). Only the right half of the anterior portion of the skull is preserved in this specimen. But it shows the posterior parts of the skull in some respects to better advantage than they are shown in the skull catalogued by the U. S. N. M. as No. 2673.

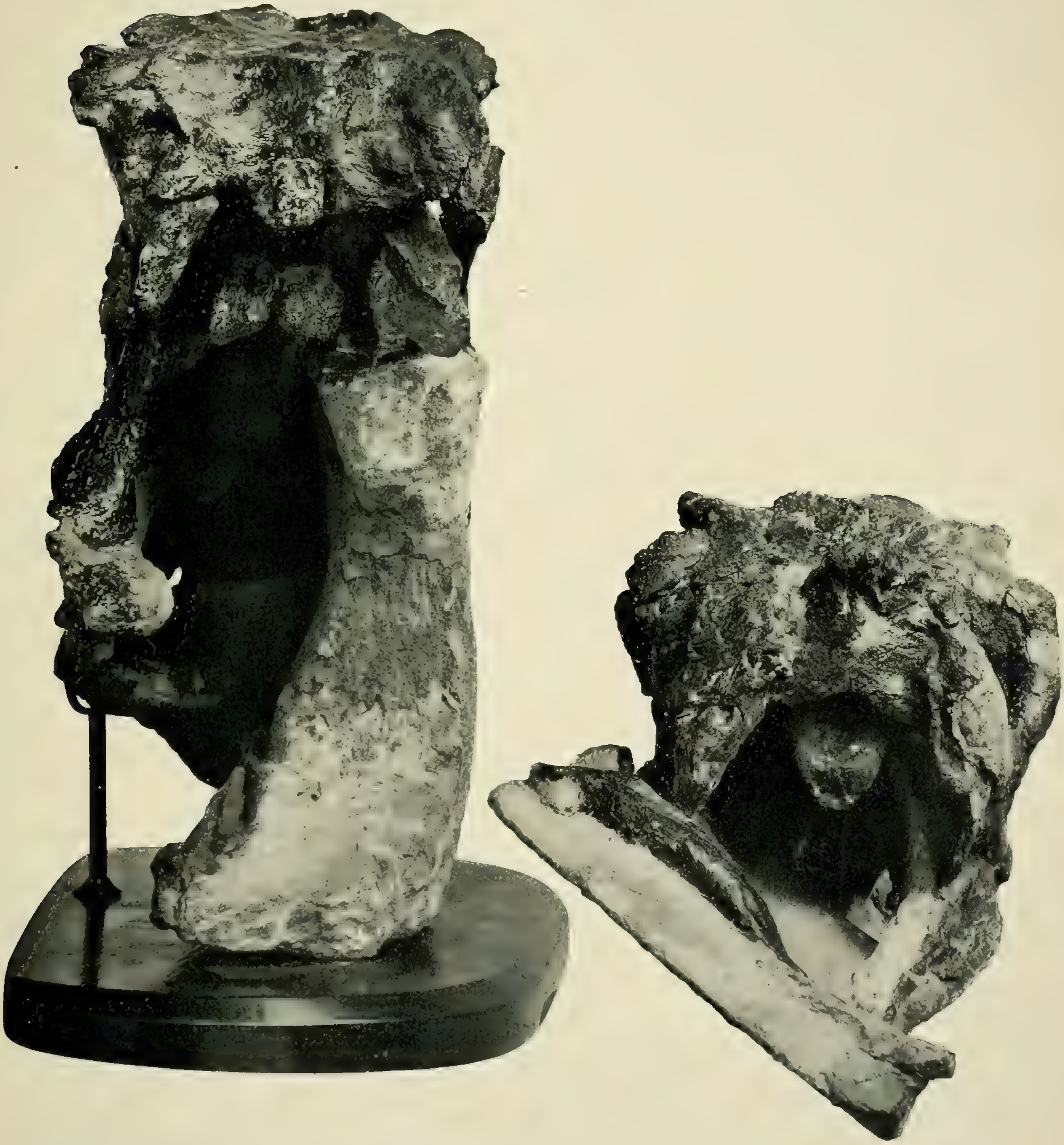


Top View of Skulls of *Diplodocus longus* Marsh, preserved in the United States National Museum.

EXPLANATION OF PLATE XXV.

The figure on the left is a view of the back of the skull of Diplodocus bearing Professor Marsh's No. 1922 (U. S. N. M., No. 2673). The basioccipital and the paroccipital processes of the exoccipitals are broken and for the most part missing, only the articulating surface of the latter remaining *in situ* on the left side.

The figure on the right is a view of the back of the skull bearing Professor Marsh's No. 1921 (U. S. N. M., No. 2672). The occipital condyle, the outline of the foramen magnum and the mode of the articulation of the bones forming the back of the skull is revealed more clearly in this specimen than in No. 2673, but there is much distortion and crushing.

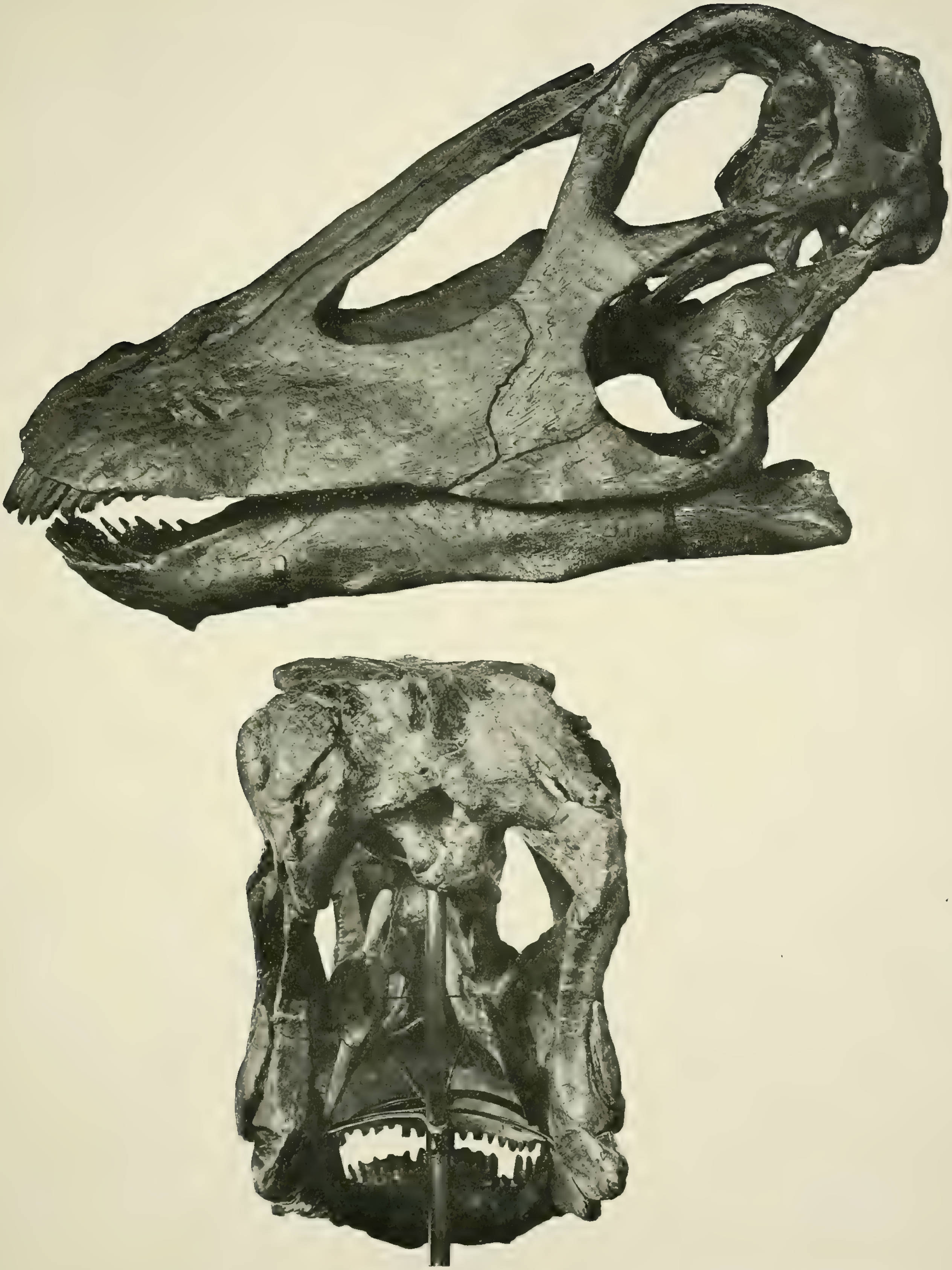


Back View of Skulls of *Diplodocus longus* Marsh, preserved in the United States National Museum.

EXPLANATION OF PLATE XXVI.

The upper figure gives a view of the left side of the skull (A. M. N. H., No. 969). A very large proportion of the superficies is artificial, and the margins of the antorbital vacuity are wholly artificial and do not conform to the outline of the type described by Professor Marsh (U. S. N. M., No. 2673). The quadrate bone at the proximal end has been broken, and appears in the restoration to show as two separate bones. The articulation of the quadrate with the quadratojugal does not agree with that shown in Marsh's type (U. S. N. M., No. 2673), and is artificial. The anterior portions of the maxillaries and premaxillaries, being largely artificial, fail to show the characteristic foramina of this region of the skull.

The lower figure gives a hind view of the same skull (A. M. N. H., No. 969).

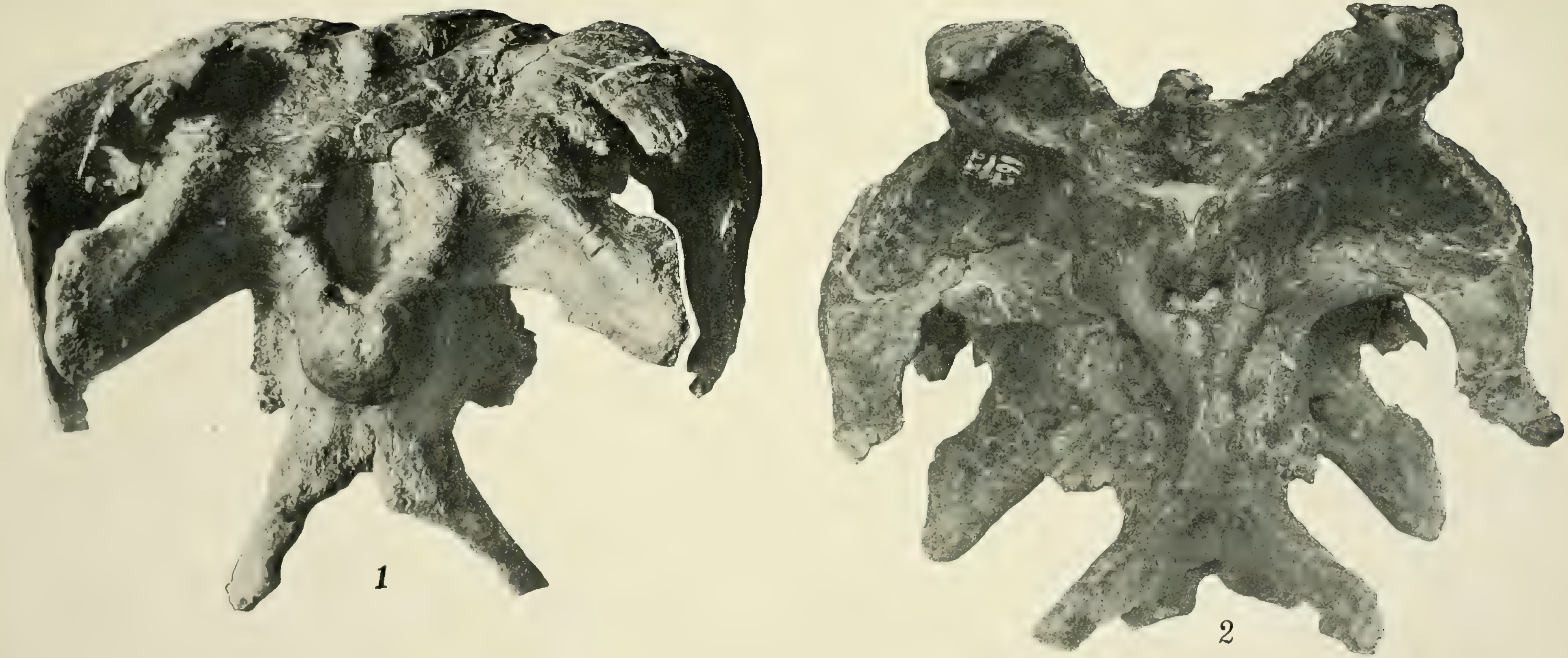


PHOTOGRAPHS OF SKULL OF DIPLODOCUS PRESERVED IN THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK (CAT. NO. 969).

EXPLANATION OF PLATE XXVII.

Fig. 1. Posterior View of the Back Part of the Skull of Specimen No. $\frac{662}{22}$, Carnegie Museum Catalogue of Vertebrate Fossils.

Fig. 2. Anterior View of the Back Part of the Skull of Specimen No. $\frac{662}{22}$, Carnegie Museum Catalogue of Vertebrate Fossils.



1

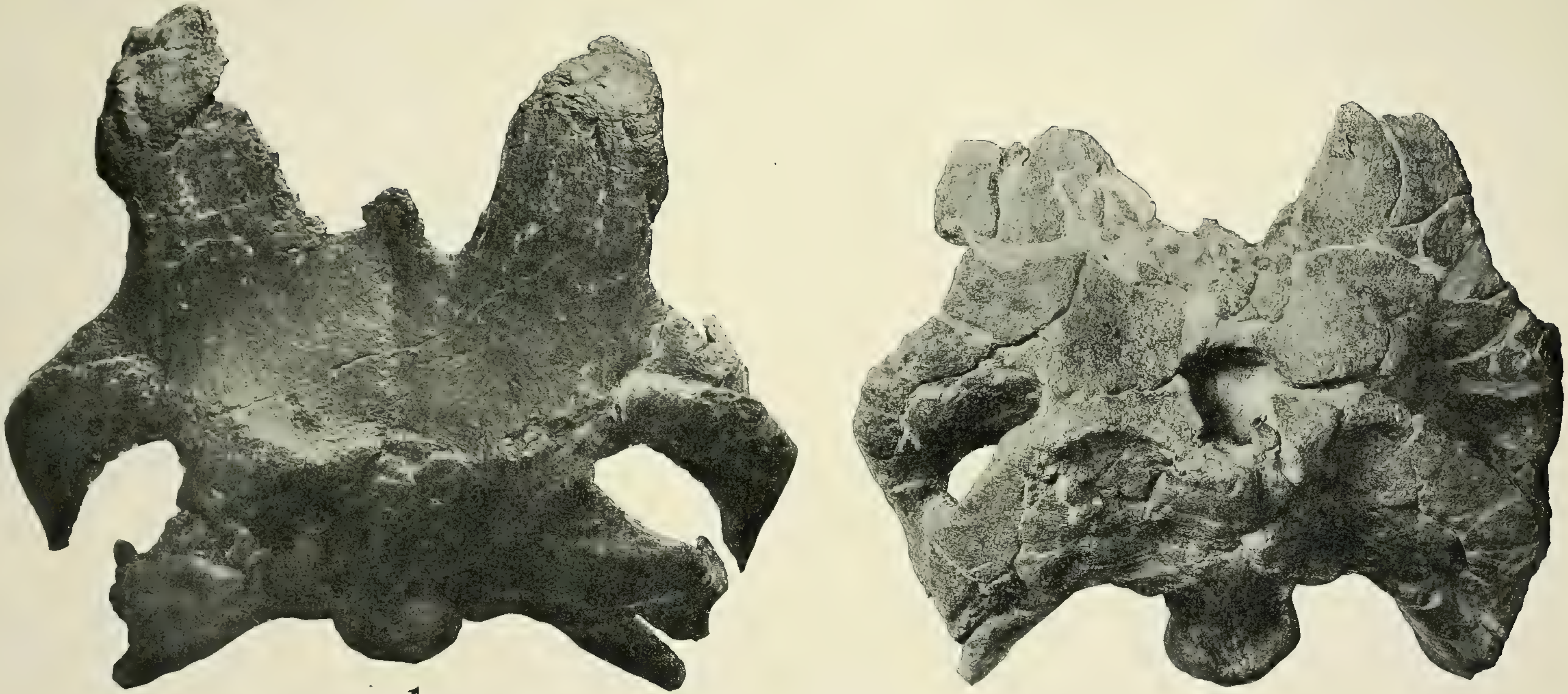
2

POSTERIOR AND ANTERIOR VIEW OF BACK PART OF SKULL OF DIPLODOCUS. (SPECIMEN NO. $\frac{662}{22}$, CARNEGIE MUSEUM CATALOGUE OF VERTEBRATE FOSSILS.)

EXPLANATION OF PLATE XXVIII.

Fig. 1. Superior View of the Back Part of the Skull of Specimen No. $\frac{662}{22}$, Carnegie Museum Catalogue of Vertebrate Fossils.

Fig. 2. Superior View of the Back Part of the Skull of Specimen No. 694, American Museum of Natural History Catalogue of Vertebrate Fossils.



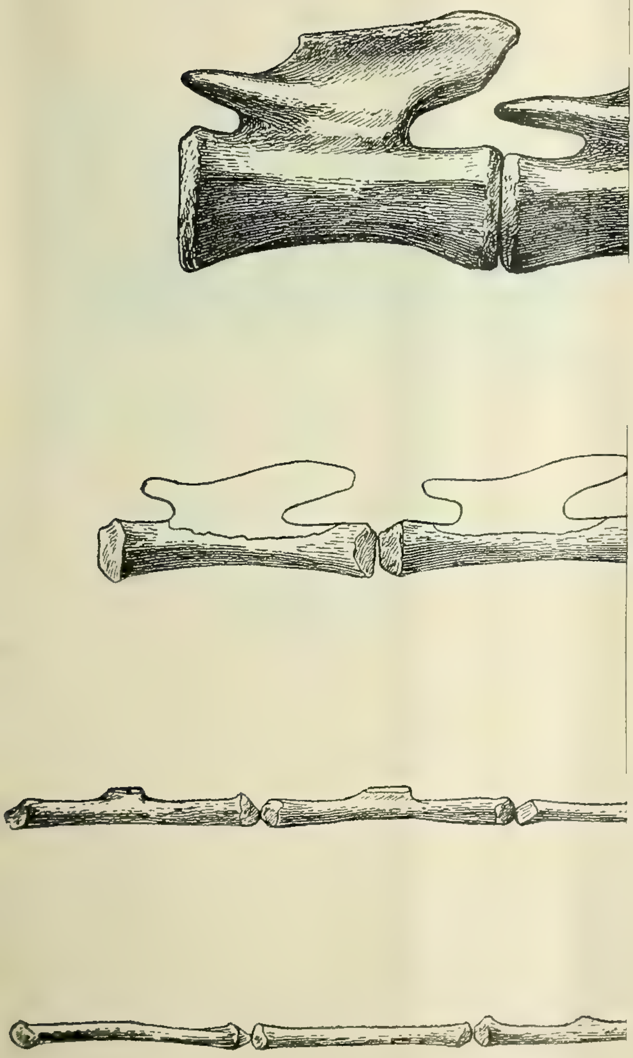
1

2

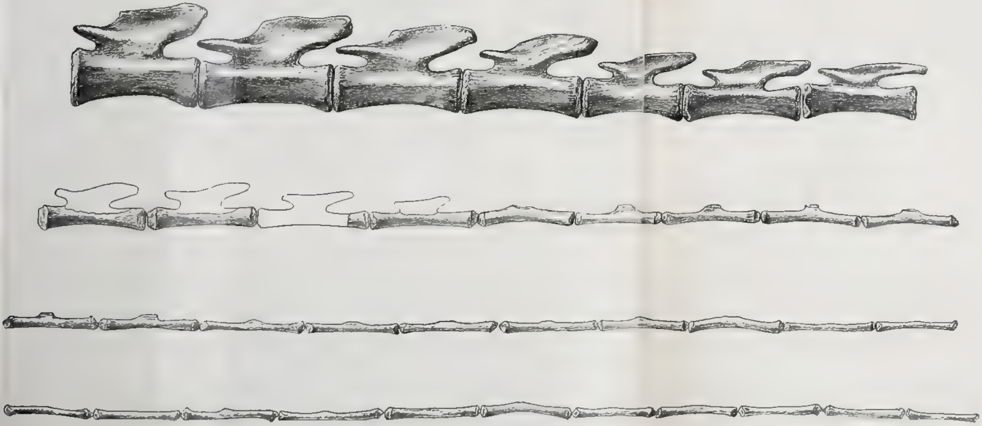
SUPERIOR VIEW OF BACK PART OF SKULLS OF DIPLODOCUS.

EXPLANATION OF PLATE XXIX.

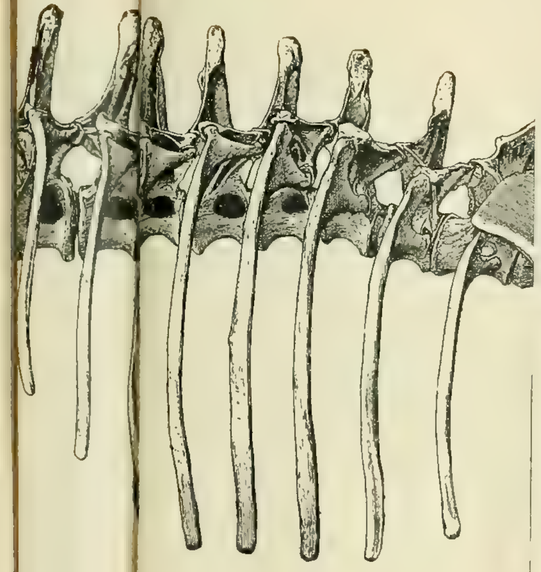
The Plate gives an outline of the caudal vertebræ (Nos. 37–73 inclusive) of the tail of a Diplodocus discovered by Mr. W. H. Utterback on the Red Fort of Powder River lying in serial order. The figures on the Plate are reduced to one fourth the natural size.



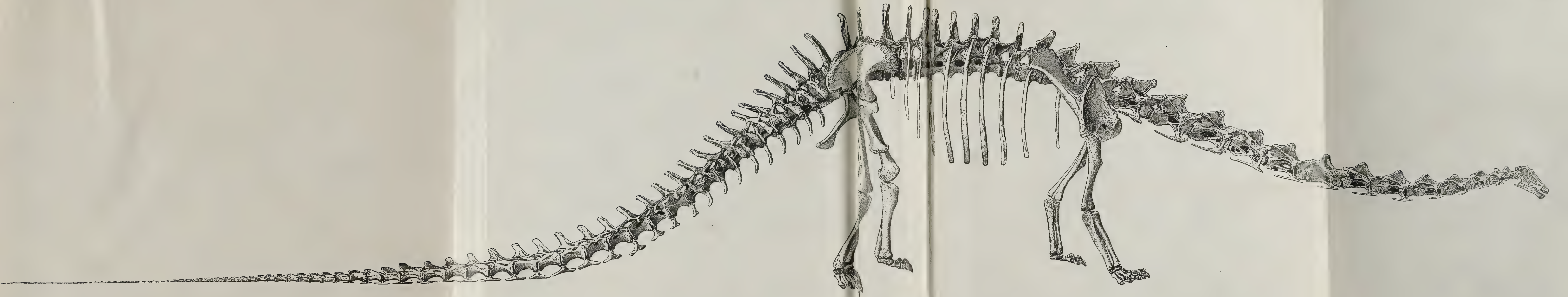
POSTERIOR CAUDAL VERTEBRÆ OF *DIPLO*



Posterior Caudal Vertebræ of *Diplodocus Carnegiei* Hatcher, Nos. 37-73 inclusive, found articulated on Red Fork of Powder River, Wyoming, by W. H. Utterback



UPON TH RESEARCHES OF J. B. HATCHER



Restoration of the Skeleton of *Diplodocus Carnegiei* Hatcher. (The drawing is based upon that given by Hatcher in the Memoirs of the Carnegie Museum, Vol. II., Plate VI., with modifications based upon thresearches of J. B. Hatcher and W. J. Holland, made subsequently to the publication of that figure, which it now supersedes.)

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 7.

THE OSTEOLOGY OF PROTOSTEGA.

By G. R. Wieland.

The first mention of ancient gigantic marine turtles from America was made by Cope in 1871 in a letter to Professor J. P. Lesley containing an account of a journey in the valley of the Smoky Hill River in Western Kansas. This letter, as subsequently published in the Proceedings of the American Philosophical Society,[1] includes a preliminary notice of the huge Niobrara Cretaceous turtle, *Protostega gigas*. The type specimen was collected by Cope himself on a bluff near Butte Creek in the vicinity of Fort Wallace. It was secured in a more or less fragmentary condition after the manner of the vertebrate collecting of the earlier days of western exploration, for, in the more extended description given in the Cretaceous Vertebrata of the West, Cope says this fossil is made up of more than eight hundred separate fragments.

The various parts of *Protostega gigas* (type), although mostly in situ, were considerably removed from their natural position. The original specimen is now in the collection of the American Museum of Natural History. It includes much crushed cranial elements with portions of the lower jaw, ten nearly free ribs, several vertebræ, various plastral elements, the shoulder girdle, a humerus, radius, and ulna, and several metacarpals and marginals, as well as parts of uncertain position. Owing, however, to the manner in which the ribs lay athwart the rather imperfect plastral plates, the latter were supposed to be dorsal, and to represent a very primitive condition of carapacial development with large fenestræ. The radius and ulna were not distinctly recognized as such although clearly figured. Owing also to a palpable numerical error in the measurements of the cranium ("$.50$ M. $= 24\frac{5}{8}$ in.") the total length of the original animal was estimated at thirteen feet, and is so referred to in text-books! The actual length is far less, as will clearly appear in the present description of a much completer cotype almost exactly the size of the original Cope specimen. This error was, however, in a sense prophetic, as some of the turtles of the related Dakotan genus *Archelon*, discovered by the writer twenty-four years after the first *Protostega*, did actually reach, or possibly exceed, the enormous size of thirteen feet in length.

---

[1] Vol. XII., p. 175.

Protostega remained a very vaguely known turtle until Baur[2] pointed out that it must in its main characteristics agree with the Cheloniidæ, and that the plates Cope supposed were dorsal must be plastral. That such was the fact was later more definitely shown by Hay,[3] who figured the nuchal and hyo- and hypoplastron of another Niobrara specimen.

The next contributions to our knowledge of the osteology of the Protosteginæ were made by the writer, after his discovery of gigantic turtles east of the Black Hills in the Fort Pierre Cretaceous in the summer of 1895. In the communications,[4] which soon followed, the structure of the greater part of the carapace and plastron was made known from remarkably preserved specimens. All the larger limb bones were also determined and figured; for the first time, indeed, in the case of any extinct sea-turtles of America. There immediately followed these papers the important contribution of Case,[5] which, in addition to a careful discussion of the systematic position of *Protostega*, added more particularly to a knowledge of the cranial characters, as based on the description of various crushed, but otherwise well defined disarticulated elements. The pelvis was also made known.

Further facts concerning the general cranial type in the Protosteginæ were next given by the writer[6] in a paper describing the splendid skull of *Archelon*, now on exhibition in the Yale Museum. Later an attempt was made by Williston[7] to restore the tarsus and give the organization of the hind flipper of *Protostega*, and by

[2] (*a*) "Die Systematische Stellung von *Dermochelys* Blainville," *Biolog. Centralblatt*, IX., 1889. (*b*) "On the Classification of the Testudinata," *American Naturalist*, XXIV., 1890.

[3] "On Certain Portions of the Skeleton of *Protostega gigas*," Field Columbian Museum Publication, No. 7, 1895.

[4] (*a*) "*Archelon ischyros*, a New Gigantic Cryptodiran Testudinate from the Fort Pierre Cretaceous of South Dakota," *Am. Jour. Science*, December, 1895. (*b*) "The Protostegan Plastron," *Ibid.*, January, 1898.

[5] "On the Osteology and Relationships of Protostega," *Journal of Morphology*, Vol. XIV. (This publication bears the date 1897, but did not appear until some time in June, 1898, its presumptively true date.)

[6] "The Skull, Pelvis, and Probable Relationships of the Huge Turtles of the Genus *Archelon* from the Fort Pierre Cretaceous of South Dakota," *Am. Jour. Sci.*, Vol. IX., April, 1900.

[7] "On the Hind Limb of *Protostega*," *Ibid.*, Vol. XIII., April, 1902.

Wieland[8] to show the carpal organization of *Archelon;* but, as will be shown below, both these efforts are almost entirely in error. From the foregoing review of the slow progress of our knowledge of the Protosteginæ it is seen that the third of a century which has elapsed since Cope's discovery of *Protostega gigas* has not sufficed to bring forth an entirely complete restoration of any single individual of these great sea-turtles. How welcome then has been the discovery during the past two years by Mr. Charles Sternberg in the Niobrara Cretaceous of Western Kansas of the nearly complete specimens of *Protostega gigas* which permit the present description of the organization of the limbs, the most important of the parts yet undescribed, as well as the least likely to be recovered in complete form. For happily the elements of the first-secured and completer of these exceptional specimens, though somewhat crushed, were found altogether, or nearly, in their naturally articulated position, a condition imperatively necessary to a satisfactory description of the flippers.

This rare fossil turtle was first briefly mentioned in *Science* by Professor Osborn[9] as "* * * a complete skeleton of *Protostega* which lay on its dorsal surface with the fore limbs stretched out at right angles to the median line of the carapace, measuring six feet between the ungual phalanges." Afterwards it was secured for the Carnegie Museum by Mr. J. B. Hatcher, who, though he crowded the brilliant work, which might well have crowned the efforts of a long life, into a short one, leaves this ripe fruition mixed with a sorrow surely not lessened by the fact that the hardships of the plains of the Northwest and the Patagonian deserts had all too plainly left their mark upon him.

Having expressed in conversation with Mr. Hatcher much interest in these more recent discoveries of *Protostega,* I was invited to make a study of the newly acquired material, this arrangement being concurred in by Dr. W. J. Holland, Director of the Carnegie Museum. But early in July, 1904, when I visited the Carnegie Museum for the purpose of doing this work, to my extreme sorrow I found, that, although I had a brief word from Mr. Hatcher shortly before, he was so seriously ill that there could be but little or no hope of his recovery. And indeed, as everyone feared, it was but a few days before he passed away. However, it was under such circumstances a relief to be busied, and Dr. Holland very kindly arranged for and furthered the initial study of the material on hand.

Furthermore, during the past summer Dr. Holland has added to the collections first obtained much additional material, also collected by Mr. Sternberg, including one very important specimen, a large *Protostega*, represented by a quite complete cranium and lower jaw, accompanied by a humerus, radius, ulna, wrist, and palmar bones — all in place on the same slab. The acquisition of this specimen has been as timely as fortunate; for it has removed all doubt as to the carpal and tarsal organization of *Protostega*, and made possible the avoidance of errors in the description of the completer specimen, most of the elements of which had been dissociated from their matrix, and the position of some of them rendered doubtful through the mistaken zeal of their collector. It will hence greatly simplify our description of the limb organization of *Protostega* as based on the free elements of the original and completer specimen, No. 1420, Carnegie Museum Catalogue of Vertebrate Fossils, if the more recently acquired and less complete *Protostega* with its parts in approximately natural position, be considered first.

---

[8] "Notes on the Cretaceous Turtles *Toxochelys* and *Archelon*, with a Classification of the Marine Testudinates," *Ibid.*, Vol. XIV., August, 1902.

[9] N. S., Vol. XIX., No. 470, p. 35, January, 1904.

Protostega gigas Cope (Cotype).

Specimen No. 1421 (*Carnegie Museum Catalogue of Vertebrate Fossils*). — This fine fossil is from the Niobrara Cretaceous of Hackberry Creek, Gove County, Kansas. The *ex situ* portions of the original skeleton, which had weathered out and were secured in more or less complete condition, include the left humerus, radius, ulna,

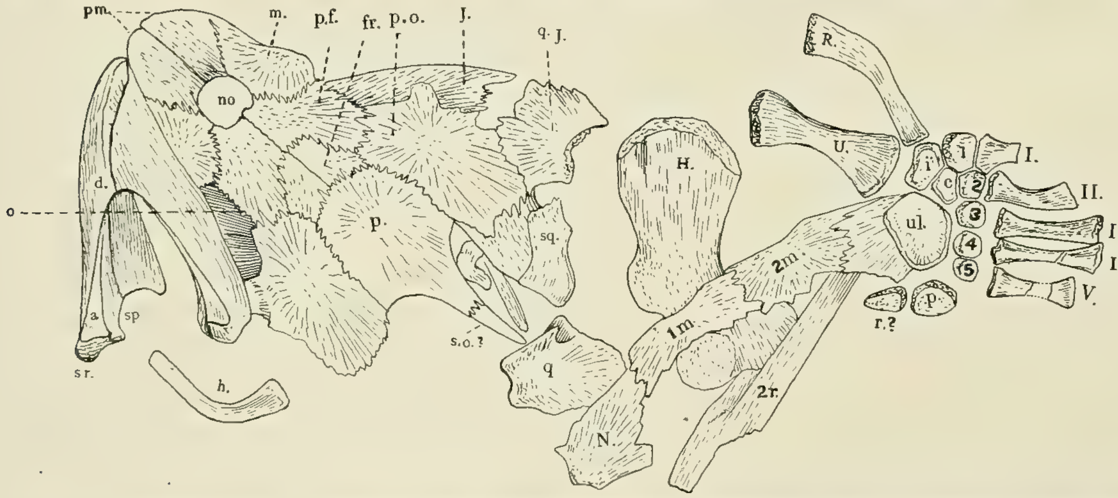


FIG. 1. *Protostega gigas.* Carnegie Museum Specimen, No. 1421, from Niobrara chalk of Hackberry Creek, Gove County, Kansas. Superior view of skull with the lower jaw and a hyoid, the right anterior border of the carapace and most of the right fore flipper, all in nearly natural position and still partially imbedded as collected on a single slab of the chalk matrix. × $\frac{1}{9}$.

Skull. — *pm.*, premaxillary; *m.*, maxillary; *n.o.*, external nares; *p.f.*, prefrontal; *fr.*, frontal; *o.*, orbital border; *p.*, parietal; *s.o.*, supraoccipital; *j.*, jugal; *q.j.*, quadratojugal; *sq.*, squamosal; *q.*, right quadrate.

Lower Jaw. — *d.*, dentalium; *a.*, angular; *sr.*, surangular; *sp.*, splenial; (*h.*, hyoid).

Carapace. — *N.*, portion of right ala of nuchal; *2r.*, second rib; *1m.*, *2m.*, first and second marginalia.

Flipper. — *H.*, humerus; *R.*, radius; *U.*, ulna; *r.*, radiale (?); *i.*, intermedium; *ul.*, ulnare; *p.*, pisiform; 1–5, first to fifth carpalia respectively; I.–V., first to fifth metacarpalia.

ulnare, radiale, and pisiform, with fragmentary phalanges, and many broken pieces of the plastron. The *in situ* portion consists of the right anterior part of the skeleton, and was secured on a single slab of the chalk matrix, in which it still remains intact, as shown in the accompanying drawing, Fig. 1, by Mr. Prentice. It includes the following : the lower jaw in oblique inferior view, with the two larger hyoidal elements ; the skull in superior view, less the left squamosal and with the right quadrate disarticulated and its anterior surface up ; the right humerus, radius, ulna, wrist, and palmar elements in superior view, and all in place, except the radiale which has slipped across to the posterior border of the wrist ; the right ala of the T-shaped nuchal with the first and second marginals, and the distal half of the second rib, all in place and resting over the proximal extremity of the humerus.

Although the various bones are more or less crushed, after the manner of most fossils from the Kansas chalk, the contours are exceedingly good. In the skull, as simply crushed down in the vertical direction with little distortion of parts, there appear in clear preservation and united by distinct sutures the premaxillaries, maxillaries, prefrontals, frontals, postorbitals, and parietals, with the right squamosal, jugal, and quadrato-jugal. The cervicals have in some way been dissociated, but the skull lies in a normal position with respect to the anterior border of the carapace, from under which the right fore-flipper projects in the normal position, the hand being bent back pronately over the position of the third marginal, part of which appears in view.

It will at once be seen what exceedingly satisfactory information is furnished by the present specimen, as compared with all other examples of *Protostega* hitherto found. The more important measurements afforded are the following :

		cm.
Lower jaw :	Extreme length of ramus	37
	Extreme length of median symphysis	16
Cranium :	Extreme length (as crushed flat) measured from end of beak to posterior extremity of occipital crest	58
	Median length of narial opening	7.5
	Greatest width of narial opening	5.5
	Orbital border of the prefrontal	6
	Antero-posterior length of orbit	12
Humerus :	Length across head	33
	Width of distal end	14
Radius :	Length	19
Ulna :	Length	18
Carpalia :	Width across the five carpalia in place	18
Metacarpalia :	(Length of 1–5 resp.) ; 7(+ or –), 10.5, 12, 12.5, 10 (+ or —) cm.	

The above cranial and hand measurements have not hitherto been obtained in *Protostega*, whence it is of interest to note, that, allowance being made for the crushing of the specimens of the Niobrara chalk, no wide differences in proportion are evident on comparison with the much larger turtles of the genus *Archelon* from the Fort Pierre Cretaceous. The lack of coössification of the mandibular rami and especially the very low radial crest of the latter form will, however, serve to distinguish it from the fossil before us. But of far greater interest than any question of generic values that may arise is the fact that the bones of the hand are, with the sole exception of the radiale, indisputably in place, the most striking feature being the immense ulnare, and the strong contact of the intermedium with the first carpale. With these remarks we may pass on, basing our main descriptions on the earlier secured and in some respects better specimen with its several elements freed from their matrix.

Specimen No. 1420 (*Carnegie Museum Catalogue of Vertebrate Fossils*). — The present specimen of *Protostega gigas* is more nearly complete than any other as yet discovered. As originally imbedded in its matrix of chalk, nearly every element was present in an exactly or approximately natural position, and recovered as follows:

1. Portions of the skull, with the crushed lower jaw and two large and well preserved paired hyoids.
2. The 1st, 4th, 5th, 6th, 7th and 8th cervical, the dorsal, sacral, and eight anterior caudal vertebrae.
3. The nearly complete series of ribs, including the anterior pair of sacral ribs, also the neurals, and various marginals.
4. The left shoulder-girdle and proximal half of the humerus, with the right shoulder-girdle and complete front flipper in place, except the ungual phalanx of the fourth and the second phalanx of the fifth digit.
5. The pelvic girdle and hind limbs complete and in place, less only the fibulare (if ossified), the ungual phalanges of the right, fourth, and fifth digits and of the left fifth digit.
6. A nearly complete though very much crushed plastron.

Unfortunately the collector of this surprisingly complete fossil, in an attempt to remove and separate the bones from their matrix of chalk, mis-marked some of them, and also made it virtually impossible to either replace more than a very few of the marginals, or to determine the outlines of any of the plastral elements with exactness. Hence it is not worth while, in view of the marked crushing undergone, to give figures of any of these parts now, although they will aid in the restoration. As will be evident to any student of the fossil vertebrates the removal of the fossil from its matrix in the absence of the necessary knowledge, training, and equipment, was ill advised. Such work is difficult enough in the best equipped laboratories. However none of the bones of the limbs are broken, and Mr. Sternberg redeemed himself by discovering and securing in such excellent condition specimen No. 1421, as just related. The position of the following parts is independently determinable :

1. The fourth to the eighth cervical, the dorsal and sacral centra, with the proximal caudal vertebrae and most of the ribs as shown in part in Fig. 2.

2. The shoulder-girdles and elements of the fore-arm ; in particular (as can be determined by actual close articulation, or by such intervening matrix as the collector permitted in much too small part to remain), the intermedium, first carpale, metacarpale and its phalanges, and also carpalia 3–5.

3. The pelvic girdle and elements of the hind flipper, in particular the *intermedio-centrale and tarsalia 1–3, and 4 and 5* (fused), as well as several metatarsals and phalanges.

It should be stated here that it is claimed that, as figured, no element of either flipper is actually misplaced, although the extent of the crushing undergone makes it quite possible that in one or two instances dorsal surfaces have been mistaken for ventral ones, or *vice versa*, and that the ends of several phalanges may have been reversed. Withal it is deemed important to be thus explicit in giving the manner in which the accompanying text-figures and photographs have been obtained, before taking up more detailed description. (Because of the compression undergone it was not thought needful to figure either the lower jaw, cervicals, or caudals. The dorsal view of the carapace can better be given after the restoration now being made.

I. The Carapace. (Fig. 2.)

With the exception of the T-shaped nuchal and the marginals with dactylate interior borders so peculiar to the Protosteginæ in distinction from all other known marine turtles, the main features of the carapace are very well represented in Fig. 2. The very thin, almost paper-like series of neuralia is present, though much crushed down on the underlying neural arches. The ribs are free through at least the distal two-thirds of their length. The first pair is comparatively slender, it not being clear as to whether, or not, their distal extremities rested on the lateral alæ-like expansions of the nuchal. The shield contour is, instead of elongate as once supposed, relatively broader than in either *Thalassochelys* or *Chelone,* the ratio of the length of the dorso-sacral series to the breadth of the carapace being as three to four.

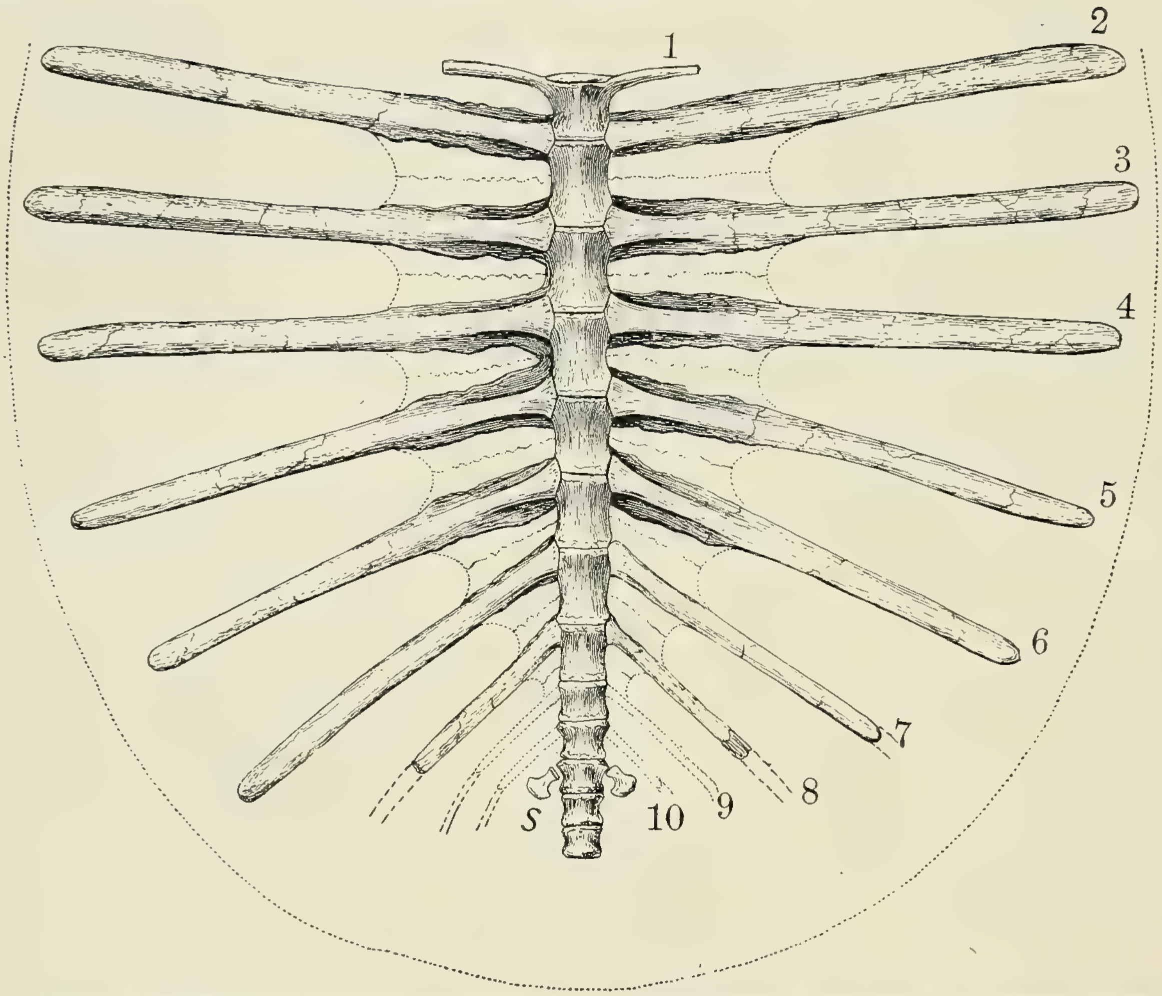


Fig. 2. *Protostega gigas.* Carapace less the nuchal and the marginal series. Inner view. 1–10, the first to tenth ribs respectively; *s*, the first sacral. Ten dorsal, the two sacral, and the first of the caudal centra are shown. (A trial drawing preparatory to mounting of specimen. About one-eighth natural size.)

This greater breadth is quite characteristic of Cretaceous turtles, and a distinct approach to a quite orbicular form like that of *Lytoloma*.[10] It is a form, moreover, that well accords with the powerful and widely expanded flippers now to be described.

II. The Front Flipper.

(Plates XXXI. and XXXII., with Figs. 3 and 4.)

The shoulder-girdle of *Protostega* is robust but presents no strongly marked peculiarities, save the elongate coracoid which extended back to the pubis as in *Eretmochelys,* but not either Chelone or the long-bodied *Dermochelys.* The features of the humerus are, however, highly characteristic, as is shown more particularly in Figs. 3 and 4, which disclose certain approximations to the humerus of *Dermochelys* not so readily discernible in the figures hitherto published. It must be noted, however, that crushing has been such as to greatly diminish the distal breadth and render it uncertain as to whether there is an ectepicondylar groove. Case speaks of a foramen in describing his specimen,[11] though his figure suggests a groove. I suspect that there may be present a true enclosed foramen rather than a deep groove as in *Archelon*. In the latter the groove is much further back from the anterior border and the ectepicondylar process correspondingly larger, while the radial crest is not nearly so prominent as in *Protostega*. (See Fig. 3.)

---

[10] Wieland, "Structure of the Upper Cretaceous Turtles of New Jersey: *Lytoloma,*" *Amer. Jour. Sci.*, Vol. XVII., September, 1904.

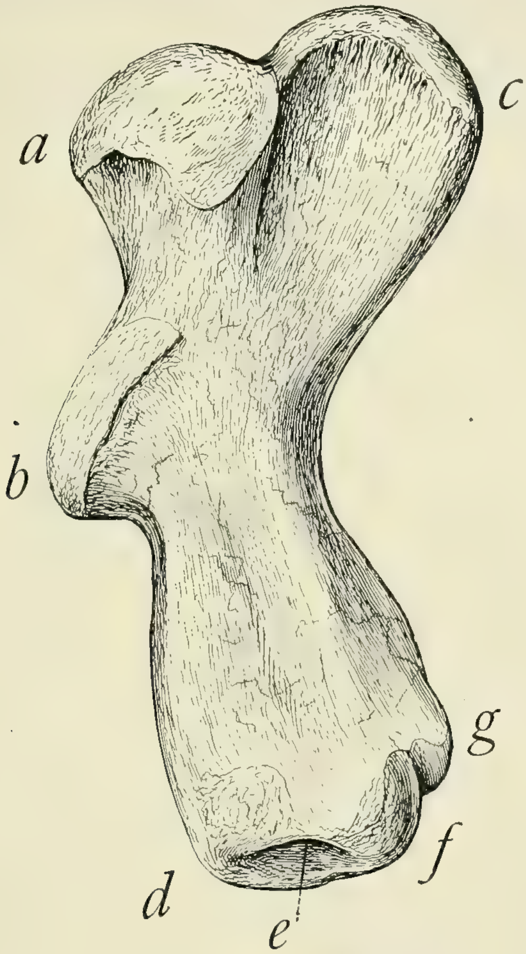


FIG. 3. *Protostega gigas*. Ental view of a large humerus. Actual length, 34 cm. *a*, head ; *b*, radial crest ; *c*, ulnar condyle ; *d*, ectepicondyle ; *e*, ectepicondylar foramen ; *f*, ectocondyle ; *g*, entocondyle.

---

[11] See foot-note 5.

The *carpal* and *finger* organization of *Protostega* has been hitherto wholly unknown, and, in fact, the only fossil marine turtle from America in which these parts have been described is *Toxochelys.*[12] In discussing the carpal organization it is of foremost importance to recall that the *intermedium*, *carpale 1*, and *metacarpale 1*, as well as *carpalia 3–5*, are still naturally articulated as in life, and in all particulars agree precisely with these same elements in specimen No. 1421. Nor is there any further doubt concerning the identification of the other elements and agreement *in toto* with that specimen. As so clearly shown in the figures and photographs, the triangular-shaped centrale articulates strongly with carpale 1. I have supposed this was not the condition in *Archelon*,[13] but must have been in error. No radiale was recovered. Bearing in mind that the several carpal elements are somewhat crushed, no further detailed description of them appears necessary, except that it should be remarked that the ulnare is of sub-hexagonal outline and relatively very large, being of the general form seen in *Thalassochelys*, and especially *Colpochelys*, rather than *Dermochelys*. The ulnare of *Archelon* is of nearly the same relative size,

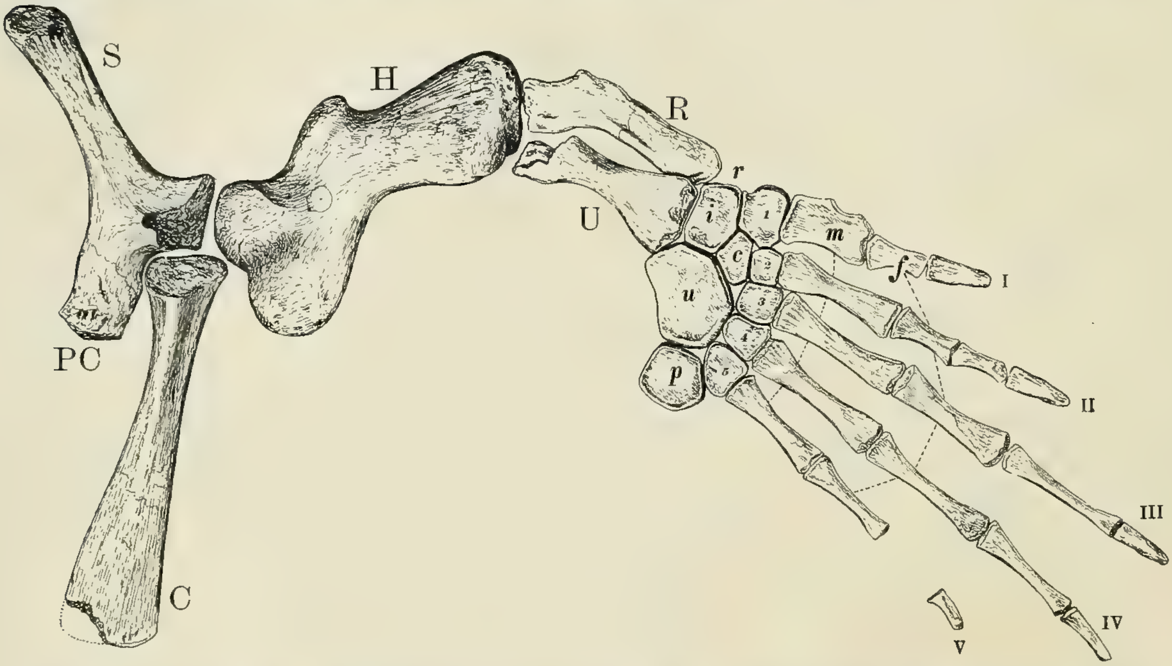


Fig. 4. *Protostega gigas.* Right shoulder girdle and flipper. $\times \frac{1}{6}$. Niobrara Cretaceous. *S*, scapular ; *PC*, procoraco-scapular ; *C*, coracoid ; *H*, humerus ; *R*, radius ; *U*, ulna ; *r*, position of the radiale ; *i*, intermedium ; *u*, ulnare ; *c*, centrale ; 1–5, first to fifth carpalia ; *p*, pisiform ; *m*, metacarpal 1 ; *p*. phalanx 1 ; I.–V., first to fifth fingers and ungual phalanges. The view is dorsal with the procoraco-scapular rotated into the plane of the paper.

---

[12] Wieland, "Notes on the Cretaceous Turtles *Toxochelys* and *Archelon*, with a classification of the Marine Testudinata," *Am. Jour. Sci.*, Vol. XIV., August, 1902.

[13] *Loc. cit.*, Wieland, "Notes on *Toxochelys* and *Archelon*," etc.

but of rounder and more regular contour. The nearly ovate pisiform is distinctly intermediate in development between that of the existing *Dermochelys* and the Cretaceous congener *Toxochelys* in which the pisiform is smaller than in any other distinctly marine turtle.

The first metacarpal is broad, and the first finger short and robust as in *Toxochelys* (see Fig. 8) and other members of the Cheloniidæ. Finger disparity is pronounced, the second finger being little elongate as in *Toxochelys*, with the third and fourth fingers of medium and nearly equal elongation, and the fifth fully as elongate as the second. The first to third fingers bore free claws, but not the fourth and fifth.

In its general features the front flipper of *Protostega* agrees much more closely with that of *Toxochelys* (Fig. 8) than with that of other forms, as one might well expect. The existing Cheloninæ do not present so close a likeness, because of the peculiar elongation of the radius and dependent carpal variations, although the boundaries are much the same, the centrale in particular being in contact with carpale 1 in both cases. With *Dermochelys*, in which carpale 1 is small and excluded from contact with the centrale, the points of likeness are more obscure, although there is no distinct suggestion in the carpal organization, that the former belongs to an utterly different race. Pisiform development is also more like that of the primitive forms than in *Dermochelys*.

The relative size of the front flippers as compared with the carapace is great, since they are not only robust, but have a spread equal to about $3\frac{1}{5}$ times the length of the dorso-sacral series of vertebræ. In the existing carnivore *Thalassochelys* this ratio is nearly as great, being equal to about three, but falls to two to one in the algaphagous *Chelone*. In the carnivore *Dermochelys* the ratio is about $2\frac{1}{2}$ to 1, a result of comparison rather unexpected in view of the very great length of fingers in the latter, and accounted for by the great length of the clipper-built Dermochelan body. There is in the comparison just made the very strongest suggestion that *Protostega*, more distinctly than any marine turtle thus far known, hunted prey, which swam actively, and, bearing in mind other features, was perhaps even powerful.

In my description of the front flippers of *Toxochelys*[14] I presented an interesting tabular comparison of the relative percentages of length of the several elements of the front flipper and humerus of various Testudinates, which exhibited the general trend of change since the Jurassic in the development and variation of flippers from a more generalized limb-type. I now include *Protostega* in this comparison. The humerus is in each case considered as having a length of 100, and the finger lengths as reduced to the same ratio, but including arbitrarily for convenience the metacarpals, as follows:

---

[14] See Footnote 8.

	Humerus.	Radius.	Ulna.	First Finger and Metacarpal.	Second Finger and Metacarpal.	Third Finger and Metacarpal.	Fourth Finger and Metacarpal.	Fifth Finger and Metacarpal.	Pisiform.
Dermochelys	100	43	39	127	180	209	173	86	23
Eretmochelys	100	53	44	49	89	128	105	44	12
Colpochelys	100	57	51	56	92	131	107	44	13
Protostega	100	60	50	50	86	128	110	80	17
Archelon.	100	54	51	—	—	—	—	—	—
Toxochelys	100	58	50	51	73	100	104	70	11
Chelydra.	100	52	53	50	72	73	55	50	small
Acichelys = (*Eurysternum*).	100	57	51	40	54	63	66	51	17

Inspection of the above table shows:

1. Strongly marked radial and ulnar decrease in length.
2. Marked tendency to radial elongation as compared with the ulna, with considerable variation in the length of the radius and ulna as compared with the humerus.
3. Nearly static length of the first finger in the *Cheloniidæ*, with a sharp increase in *Dermochelys*.
4. That elongation of the second finger appeared slowly.
5. Early and persistent increase in the length of fingers three and four.
6. More or less variable tendency to elongation of the fifth finger, with a sharp increase in *Dermochelys*, and a suggestion that this finger may have first elongated in some forms, and then undergone decrease in length.
7. Great and persistent pisiform increase, which began relatively early.
8. Increased finger disparity is mainly coördinated with depression of the radial crest.

III. The Hind Flipper. (Fig. 5.)

The presence of an entire pelvis and the complete hind flippers, save only the ungual phalanges of the right second digit, and of both fifth digits is quite all that the most exacting anatomist could wish. Although as the result of compression in the matrix the bones are of slightly broader outline than in life, their proportions are, as in the front flippers, fairly well retained. Likewise, as is so often and so fortunately the fact in the fossils from the Kansas chalk, most of the articular facets and surface characters are, as in the other parts of this excellent specimen, clearly indicated.

Regarding the pelvis it is only necessary to note that the obturator foramen must have been completely enclosed by the close contact of the ischium and entopubis on the median line as in *Archelon*.[15] The figures given herewith would not of themselves be quite clear upon this point were it left unnoticed. The ilia are of course shown in the lateral view; this, as the result of compression, being the only view remaining in fairly exact proportion.

---

[15] Wieland, *loc. cit.*, "The Skull and Pelvis, etc., of *Archelon*," p. 247.

Similarly the left fibula, as shown in Plate II., is turned partly around with a portion of the plastron adhering, the facet for contact with the distal end of the tibia being thus directed upwards. There can be but the barest doubt that the position of all the elements of the hind flippers as assigned in the accompanying Fig. 5 is correct. The presence of paired parts afforded a means of so exactly checking the determinations as to exclude all possibility of error. Moreover, nearly all the parts, save perhaps the two ulnares, were imbedded in their matrix in a closely articulated natural position. *And it should be noted that the tibiale, all the tarsalia, and the first metatarsal and some of the phalanges of both flippers remain so articulated,* the evidence as to their position hence being incontestable. Also metatarsal V., though not articulated, or otherwise joined by remaining matrix, is of such characteristic form as would testify amply to its position, even though isolated. The same may be said of metatarsal 1. The development is in both cases much the same as in all the marine turtles. Unfortunately, however, no element referable to a fibulare, which appears to have been present, is now determinable. Nor is a

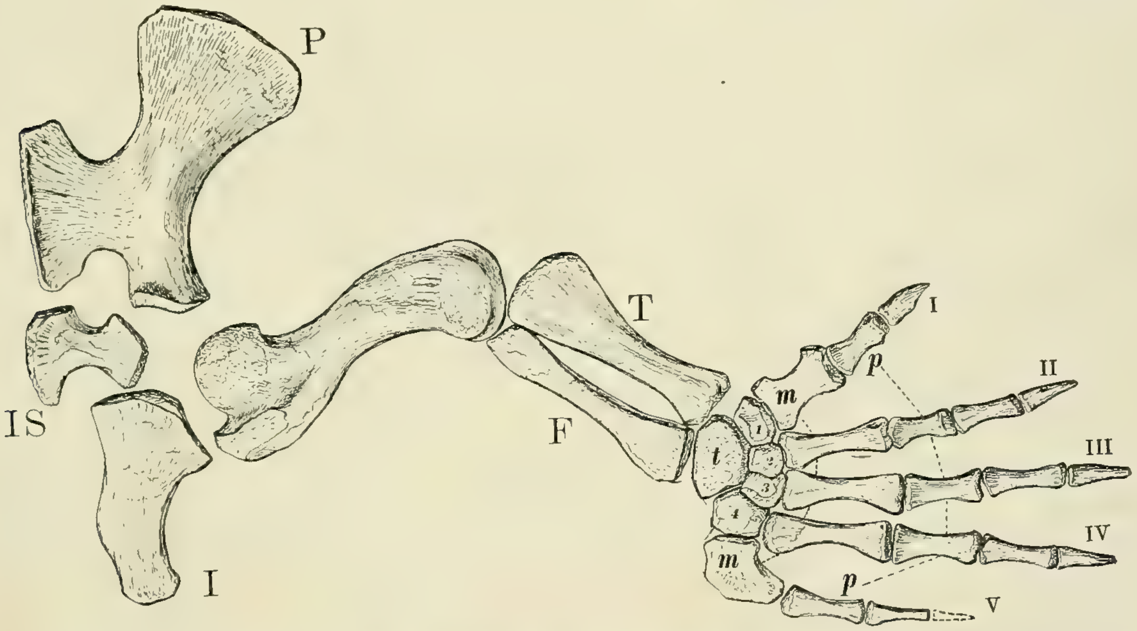


FIG. 5. *Protostega gigas.* Right pelvic girdle and flipper. × $\frac{1}{6}$. The dorsal or ectal view of flipper with the corresponding ental view of the pelvic elements show in the plane of the paper. *P*, pubis; *F*, fibula; *t*, tibiale intermedium and centrale fused, or calcano-astragalar element; 1–3, first to third tarsalia; 4, fourth and fifth tarsalia fused; *m*, metatarsal 1; *p*, phalanx 1; I.–V., first to fifth toes and ungual phalanges.

fibulare represented in the drawing, it being difficult to determine what may have been its outline.

The first toe is short, the second, third, and fourth of nearly similar moderate elongation, and the fifth somewhat elongate, as set on the strongly bowed and enlarged metatarsal V., which is similar to that common to all sea turtles.

The first toe bore a heavy and free claw, and I believe the claws of toes II.–IV. were also free and clawed, as indicated by their form and the curvature of the antero-lateral or ungual ridges. Reference may be made to Fig. 6, showing the lateral view of all the ungual phalanges which were all dissociated.

Allusion has been made to Professor Williston's restoration of the hind limb of *Protostega*,[16] and, before passing on to a general comparison with other forms, it is necessary to deal with this restoration more specifically. Williston's figure is that of a form so different from *Protostega* and all other turtles, that, if correct, it would indicate the existence of a new and hitherto unknown genus, or even family, of marine turtles. But this cannot be; for the form and proportions of the individual elements is throughout essentially the same as in *Protostega*. The fact is that the arrangement of elements given by Professor Williston affords no approximation, and no direct hint as to the tarsal organization in *Protostega*. Metatarsal V. is placed in the position of metatarsal I., and the bone supposed to be metatarsal V. is probably from another animal, or else, the metatarsal of the other flipper is much altered by the compression to which nearly all the turtles from the Kansas chalk have been subjected. The other tarsals are difficult to adjust, although it is in particular likely that the element placed in the fibular position is a pisiform; for in both form and proportions it agrees with the pisiform of both of the present specimens, and differs very markedly in these respects from the true tarsal elements. The phalangeal

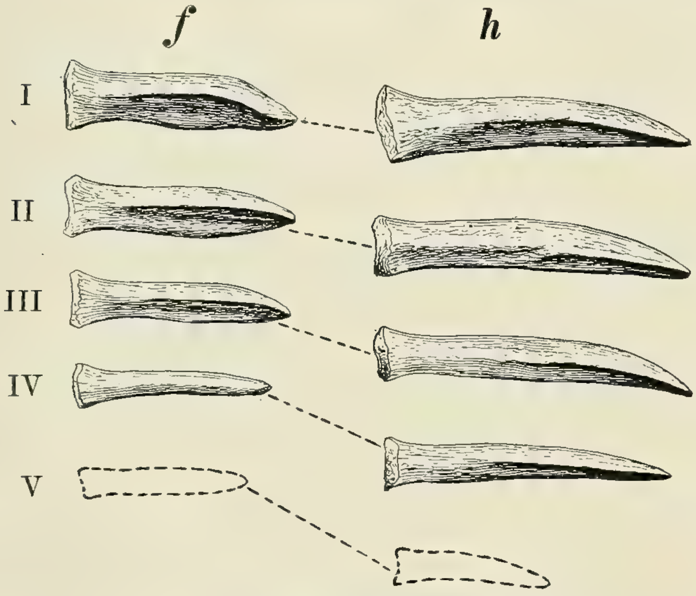


FIG. 6. *Protostega gigas*. Ungual phalanges. *f*, fingers; *h*, toes. Lateral view. × $\frac{2}{3}$. (Trial series not found to necessarily be the exact finger and toe series.)

---

[16] See foot-note 7.

formula of 3, 3, 3, 3, 0, as proposed by Williston, is not that of *Protostega,* in which the true formula is 2, 3, 3, 3, 3.

The strongly marked angular tubercle of the proximal end of the fibula, as figured by Williston, reminds one of the similar and similarly situated process on the femur of the Dinosaur, *Camptosaurus.* It is not present in any of the specimens of *Protostega* known to me, and must at least indicate a new specific form. Should further examination confirm the presence of this feature, the specimen in the collection of the University of Kansas, which shows it, should be known as the type of a new species. And surely its most appropriate name would be one honoring the distinguished paleontologist who first studied it, and who rendered a very distinct service by figuring it as best he could in the absence of further material or means of checking results.

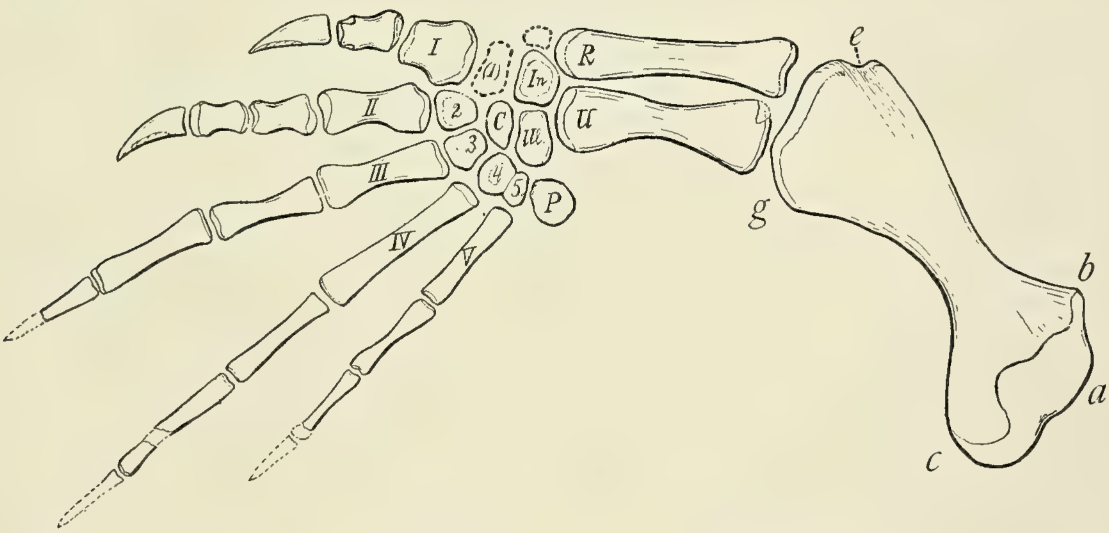


FIG. 7. *Toxochelys latiremis.* Left front flipper. Dorsal view. *a*, head; *b*, radial condyle; *c*, ulnar condyle; *e*, ectepicondylar groove; *g*, entocondyle; *R*, radius; *U*, ulna; *In*, intermedium; *Ul*, ulnare; *C*, centrale; 1–5, first to fifth carpalia; *P*, pisiform; I.–V., first to fifth metacarpals and fingers.

Structurally, aside from the more primitive clawed condition, there is no hiatus between the tarsal and other features of the hind flipper of *Protostega* and the existing sea-turtles, the comparison with *Dermochelys* being quite as close as any other, in some respects closer in fact than with a somewhat aberrant although primitive form like that of *Colpochelys* (Fig. 8). In *Dermochelys* and *Protostega* the relative size and development of all the tarsal elements is suggestively alike. It is indeed increasingly difficult to believe that the former genus belongs to an utterly remote and primitively separated line. But unfortunately there is not yet known amongst the fossil marine turtles a single hind flipper which is sufficiently well preserved to afford further detailed comparison with *Protostega.* The writer has, however, pointed out the fact that the littoral, or semi-marine, turtles of the Cretaceous of New Jersey, especially *Osteopygis* and *Lytoloma,* present many interesting primitive features, amongst these being relatively longer hind limbs, the inference being a quite clear one, that in the evolution of the limbs of the marine turtles, in correlation with carapacial and other changes, the hind limbs underwent shortening, and the front limbs a compensatory elongation. In fact in *Osteopygis,* a form now known to be very closely related to the ancestors of the Cheloninæ, the femur is distinctly longer than the humerus, as is also the case in *Chelydra,* a tortoise which is in many respects suggestive of specialization in some direction similar to that doubtless followed by the direct ancestors of the marine turtles. In *Lytoloma,* an upper Cretaceous and lower Eocene genus closely related to *Chelone,* the femur appears to have undergone some

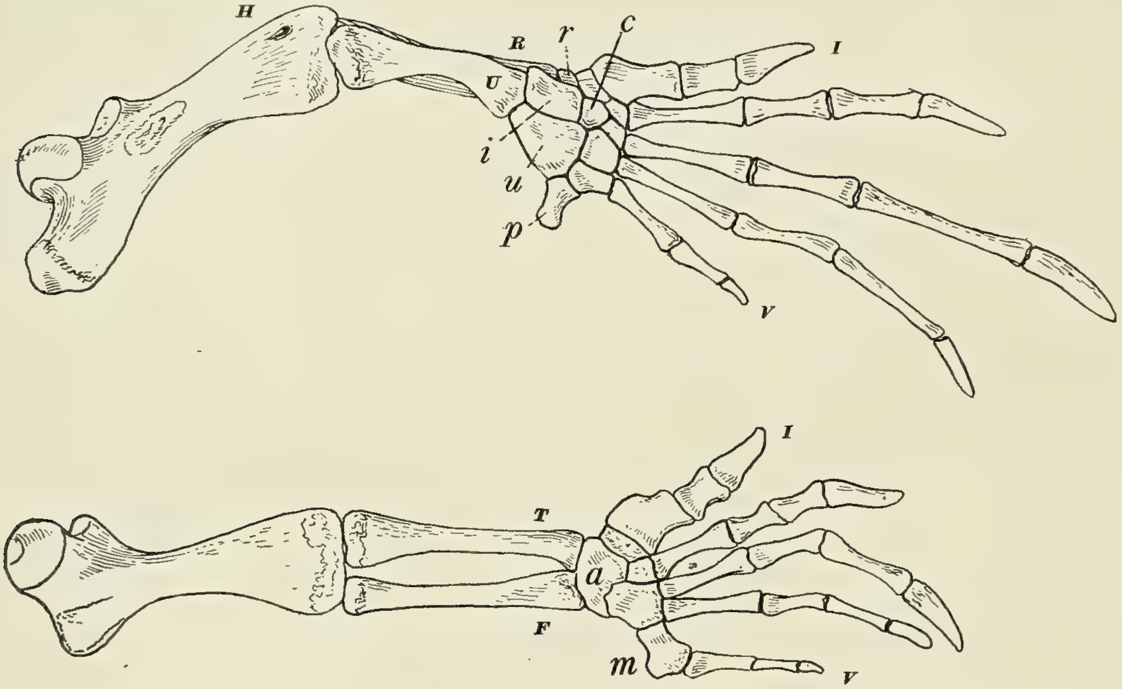


FIG. 8. *Colpochelys Kempi* Garman. $\times \frac{3}{8}$ Fore and hind flipper of a specimen in the United States National Museum (ratio of fore to hind flipper, 1.25).

Fore Flipper. *H,* humerus with ectepicondylar perforation set well in from the anterior border: *R,* radius in natural position revolved somewhat beneath the ulna (*U*); *r,* radiale, bounded by the radius, the intermedium and first carpale; *i,* intermedium, *u,* ulnare; *p,* pisiform; *c,* centrale bounded by the intermedium, ulnare, and first to fourth carpalia; I., V., first and fifth fingers.

Hind Flipper. *T,* tibia, *F,* fibula; I., V., first and fifth toes. The tibia and fibula support a single heel or astragalo-calcaneal element, (*a*) theoretically formed by the fusion of four elements corresponding to the radiale, intermedium, ulnare, and centrale. The first toe is borne on tarsale I., the second on tarsale II., and the third to fifth on tarsalia III.–V., fused. Metatarsal 1 (*m*) is the exact equivalent of metacarpal 1, and metatarsal V. has a pisiformoid development.

relative shortening. But though a nearly complete carapace has recently been described,[17] in the absence of further description of the Belgian material, now in process of elaboration by M. Dollo, we know very little of the limb development in this form, except by inference. In the case of *Toxochelys*, which is near to *Lytoloma*, we fortunately know the organization of the front flipper within close limits (cf. Fig. 7), while I have but recently described the carapace of a most interesting new species, *T. Bauri.*[18] In *Toxochelys* we find a markedly primitive form of flipper, indeed the most primitive known, although the humeral contour and finger disparity indicate an animal capable of navigating the open seas. Also, the carapace of all the Toxochelyds known has very large fontanelles, suggesting a marine life quite as decidedly as the flipper; for though the laws of carapacial reduction are as yet only surmised, it is only in the marine members of the Cryptodira that prominent pleuro-marginal fontanelles occur.

Because of the facts given it does, however, prove decidedly interesting to find that even in *Protostega* of the Upper Cretaceous, the hind limbs yet remain relatively long, though fully developed as flippers. For in *Eretmochelys* and *Chelone* as well as in *Dermochelys*, the fore flippers vary from about 1.55 to 1.60 times the length of the hind flippers; whilst in the orbicular bodied *Protostega*, with a tremendous spread of front flippers as already pointed out, this ratio falls to 1.30, which is, however, a little in excess of *Colpochelys*. In the latter genus which has in some respects the most primitive flipper organization of any existing Cryptodiran the fore flippers are but 1.25 times the length of the hind flippers. Doubtless there are many further interesting numerical relationships not yet discovered. Though the relatively strong pattern and great size of both fore and hind flippers in *Protostega* and the related *Archelon*, taken with the broad body and shortness of the dorso-sacral series, may not indicate extreme and sustained swiftness, in conjunction with the cranial features these proportions do go far to confirm the opinion already expressed that these turtles, so powerfully equipped for both swimming and attack, may well have hunted actively swimming prey. The Protosteginæ plainly included the largest and the most rapacious turtles which ever existed.

---

[17] Wieland, "Structure of the Upper Cretaceous Turtles of New Jersey; *Lytoloma*," *Am. Jour. Sci.* September, 1904.

[18] Wieland, "A New Niobrara *Toxochelys*," *Am. Jour. Sci.*, November, 1905.

IV. Systematic Position of Protostega.

CHELONIODEA (Baur).

(Superfamily of the Cryptodira.)

A parieto-squamosal arch; palatine foramen and free nasals sometimes present, (Desmatochelydinæ); fourth cervical biconvex, with the centra of the sixth to eighth much more modified in recent than in most Cretaceous forms.

(*A*) Dermochelydidæ.

No descending parietal processes; no palatine foramen; other cranial and limb characters not remote from those of the Cheloniidæ; carapace represented by the nuchal only, and body enveloped in a leathery hide with an osteodermal mosaic; no claws. Genera: *Dermochelys*, *Psephophorus*, *Eosphargis*.

(*B*) Cheloniidæ.

Skull with descending processes of parietals, so far as known; palatine foramen sometimes present; vomero-premaxillar union usual but not constant; a normal, though often much reduced carapace and plastron; nuchal with or without articular process on under side; claws one, two, or more.

1. *Protosteginæ* (Wieland): No free nasals, and no palatine foramina; obturator foramen small and enclosed by ischio-pubic contact on the median line, as in many land forms; nuchal T-shaped; neuralia and pleuralia thin and investing the ribs but slightly; marginalia usually spiniferous on interior borders; plastral elements of medium development with numerous digitations on both outer and inner border of the hyo- and hypoplastron; epiplastron of Trionychoid and Acichelysoid form; body enveloped in a leathery hide (?); claws three or more.

(*a*) *Protostega* Cope. — Cranial elements nearly as in *Archelon;* mandibular rami coössified; radial process of humerus strong; front flippers very broad and of a more distinctly marine type than those of the Toxochelydinæ (*Toxochelys*); centrale in contact with carpale 1; hind flippers relatively very large, and tarsal region most like that of *Dermochelys*. Species: *P. gigas* Cope from the Niobrara Cretaceous of western Kansas:

Ratio of spread of front flippers to length of the dorso-sacral series	3.2
Ratio of front to hind flipper	1.3

First to third fingers free, clawed.
First to fourth toes free, clawed.

V. Measurements of Protostega gigas.

(All based on the single individual illustrated in Text-figures 2–7 and Plates I. and II. As most of the elements are much flattened lengths only are given, these doubtless remaining much the same as in life.)

(*A*) *The Lower Jaw.*

Length on median line (estimated, the tip being broken away)	26	cm.
Length along ramus	30	"

(*B*) *The Carapace, Ribs and Dorso-sacral Centra.*

Total length of the ten dorsal centra	68	"
Total length of the three succeeding centra	10	"
Length of the dorso-sacral series	4.5	"
Extreme width of the carapace (exclusive of marginals) as crushed out flat and measured from tip to tip of the fourth ribs, both of which are complete and are the longest of the rib series	106	"
Length of the first to tenth dorsal centra respectively, 5.5, 7.5, 8, 8, 9, 8, 7.5, 6.5, 4, 4		"
Lengths of the first and second sacral and first caudal centra respectively, 3, 3.5, 3.5		"
Lengths of the first rib	10 +	"
" " second rib	49	"
" " fourth rib	51	"
" " fifth rib	51	"
" " sixth rib	46 (?)	"
" " seventh rib	43 (?)	"
Length of first sacral rib (in place)	3.2	"

(*C*) *The Shoulder Girdle.*

Distance apart of the two distal extremities (the scapular and the precoracoidal) of the procoraco-scapular	30	"
Length from interior bow of procoraco-scapular to the glenoid cavity	13	"
Length of the coracoid	40	"

(*D*) *The Pelvic Girdle.*

Length of pubis (outer exterior border, on straight line)	18	"
Length of ischia	8.5	"
Length of ilium	18	"
Length of pelvis on median line	43.5	"
Width across pubis at broadest point	48	"

(*E*) *The Limbs.*

The greatest spread of the front flippers (as based on measurement from the approximate median line of the shoulder girdles to tip of longest finger)	250	"
Greatest spread of hind flippers	190	"

(1) *The Front Flipper.*

Length from glenoid cavity to tip of finger III	106	"
Length of humerus	34	"
Length of radius	20	"
Length of ulna	17	"
Length of intermedium	7.5	"
Width of intermedium	4.5	"
Length of carpale 1	6	"
Length laterally across carpalia 3–5, which remains as recovered naturally articulated.	10.6	"

Length of ulnare	10	cm.
Greatest width of ulnare	7	"
Length of pisiform	6.1	"
Length, inclusive of metacarpals, of		
First finger	18	"
Second finger	29.5	"
Third finger	43	"
Fourth finger	39	"
Fifth finger	30	"

(2) *The Hind Flipper.*

Length from acetabulum (or head of femur) to tip of finger III	85	"
Length of femur	27	"
" " tibia	20	"
" " fibula	20 5	"
" " tibiale	7	"
Greatest length of the first to fourth tarsalia as they yet remain naturally articulated (on line across ankle)	11	"
Length, inclusive of metatarsals, of		
First toe	18	"
Second toe	27	"
Third toe	30.5	"
Fourth toe	31	"
Fifth toe	20	"

EXPLANATION OF PLATE XXXI.

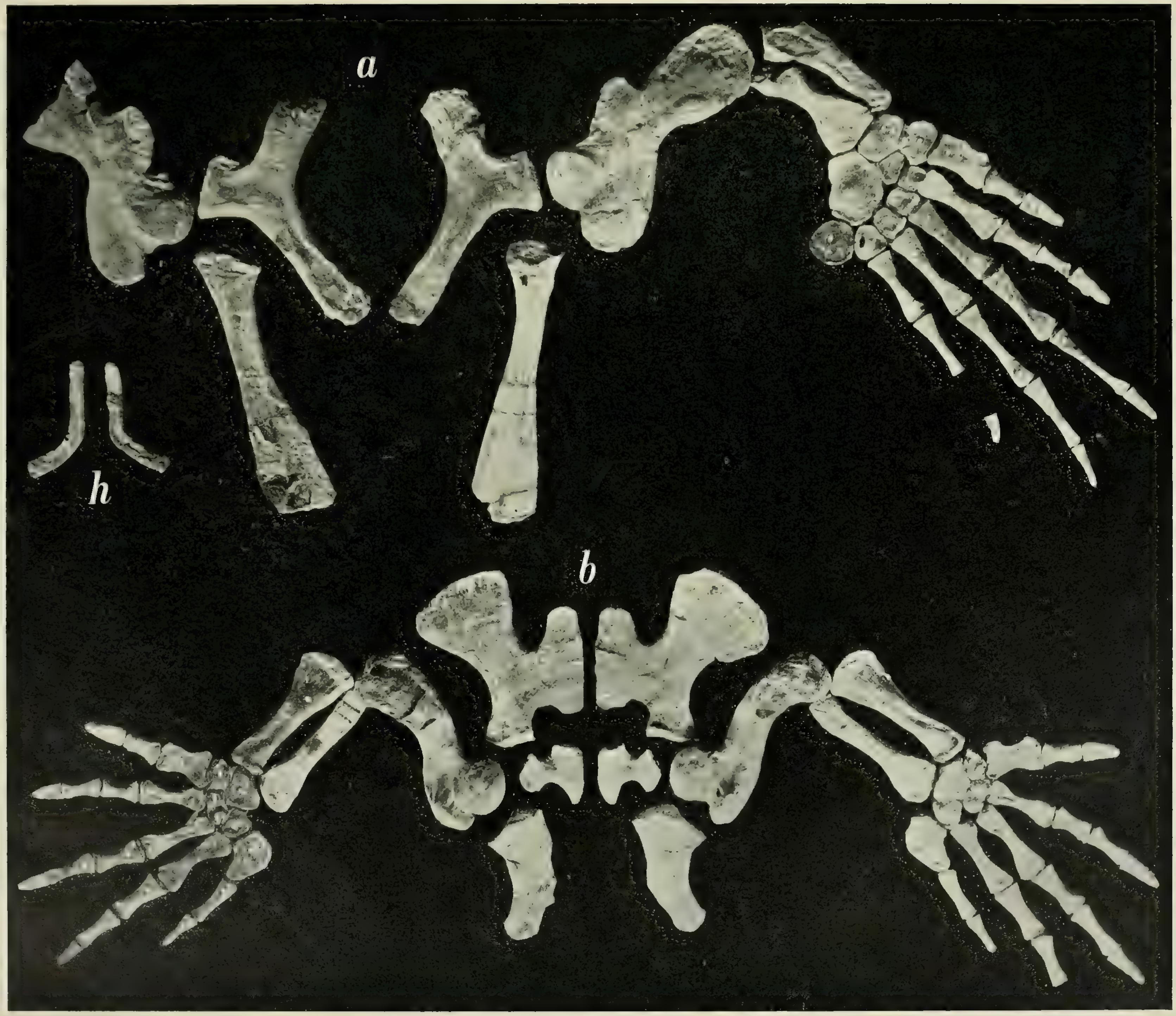
Protostega gigas. (Carnegie Museum. Cat. Vert. Fossils, No. 1420.)

(*a*) Right and left shoulder girdles, with right front flipper and the proximal half of the left humerus.

(*b*) Pelvic girdle with both hind flippers.

(*h*) The accompanying hyoids.

The elements are shown as photographed in superior view in approximately the position in which they were imbedded and crushed out flat in the matrix of chalk. All the elements belong to a single individual from the Niobrara Cretaceous of western Kansas.



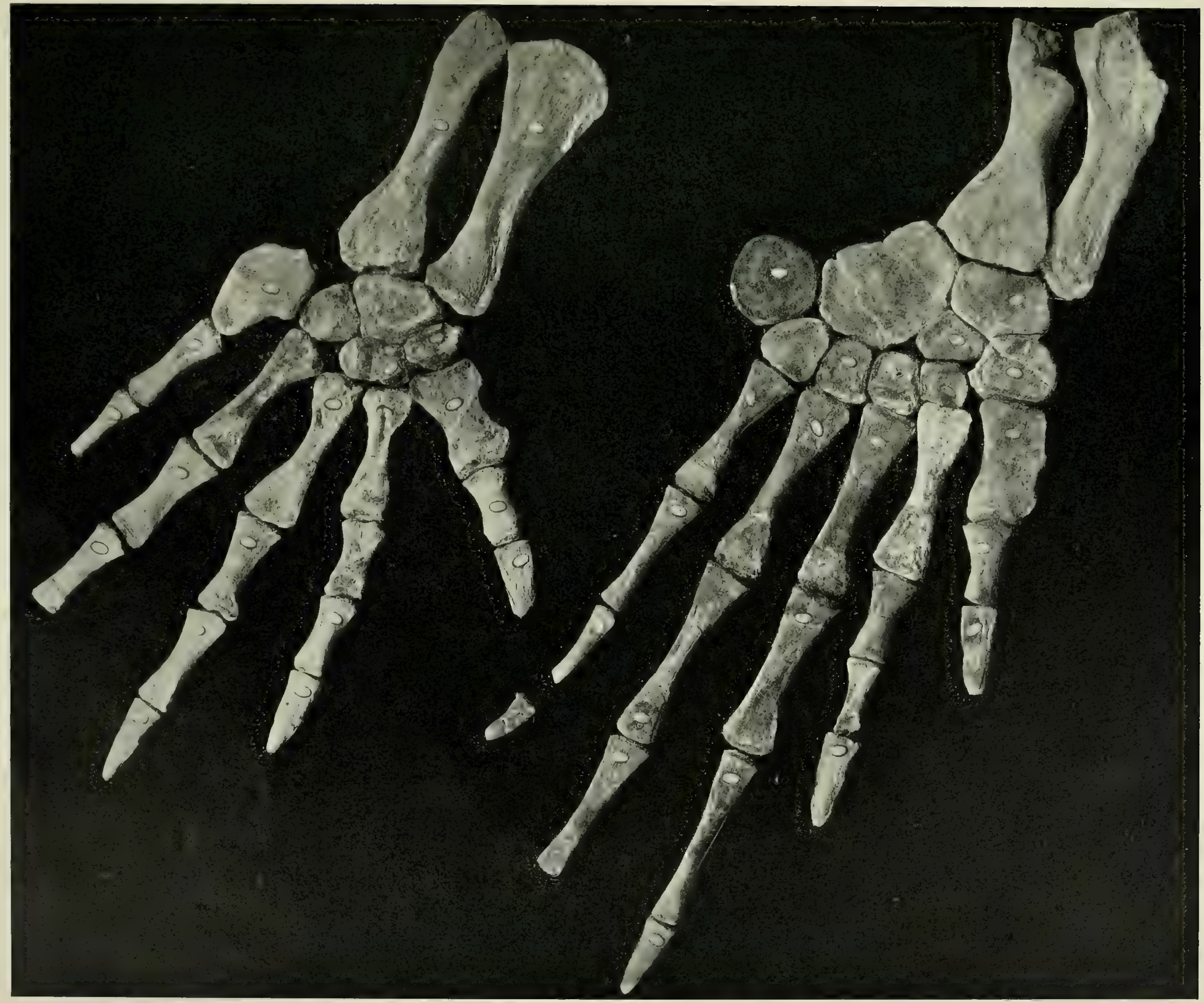
PROTOSTEGA GIGAS COPE.

EXPLANATION OF PLATE XXXII.

Protostega gigas. (Carnegie Museum. Cat. Vert. Fossils, No. 1420.)

Enlarged views of forearm and hand (upper photograph), and the foot (lower photograph).

Observe in the *upper photograph* that the intermedium, carpale 1, and metacarpale 1, as well as carpalia 2–4 are still articulated as in the matrix ; and in the *lower photograph* that the tibiale with tarsalia 1–5 and metatarsal 1 are likewise articulated as found in their normal position in the matrix.



PROTOSTEGA GIGAS COPE.

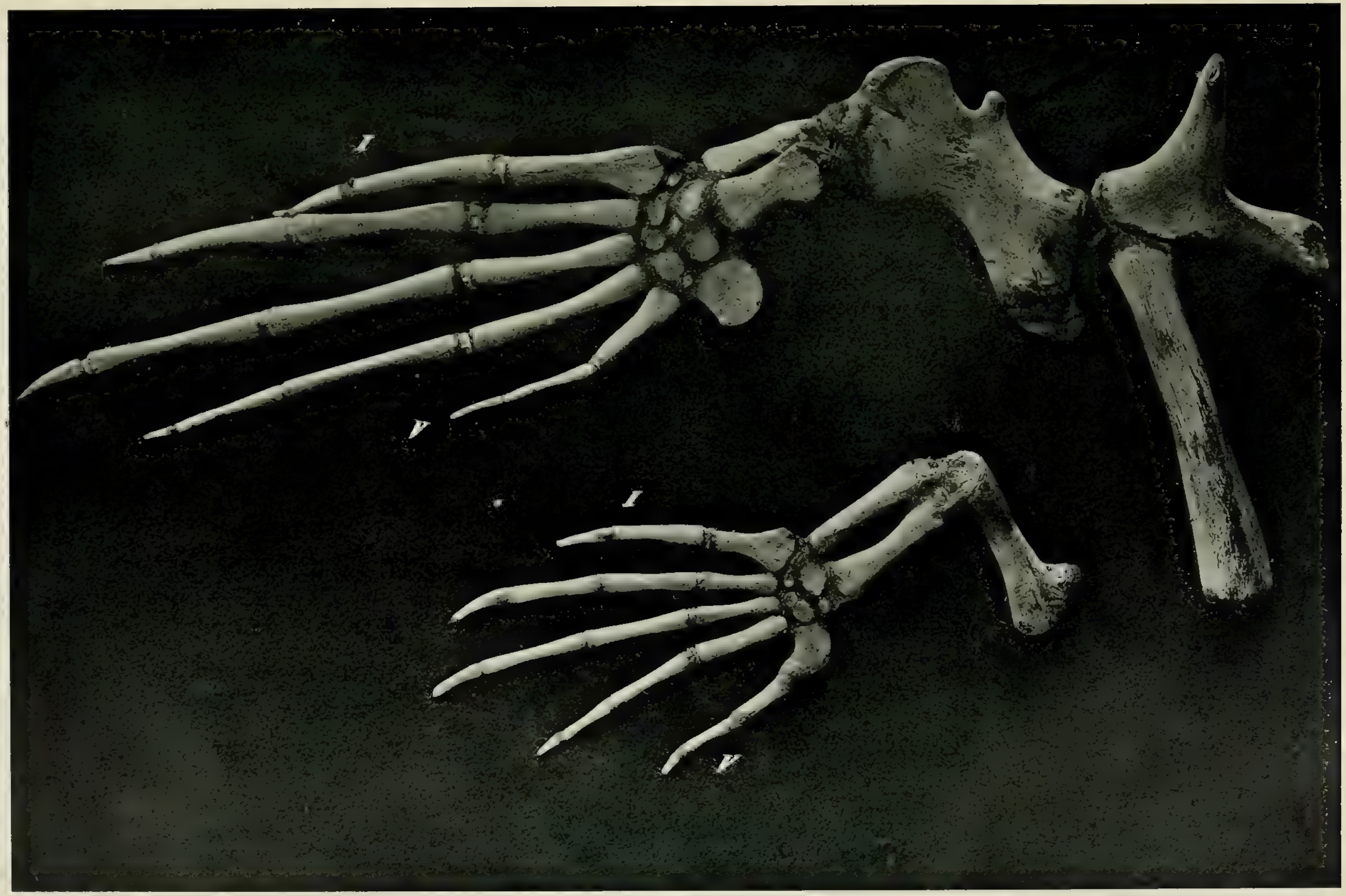
EXPLANATION OF PLATE XXXIII.

Dermochelys coriaceæ.

(*a*) Shoulder girdle with front flipper articulated, and the procoracoscapular thus shown foreshortened.

(*b*) Hind flipper. Superior view.

I., V., the first and fifth fingers and toes respectively.



DERMOCHELYS CORIACEA.

K $^{+}$N 90 6031 [General]
6027 gi [Nebraska] 6000

Peterson etc.

[K 90.6031 gi $^{+}$N 6027 gi 6031]
[Ungulata]
)

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 8.

NEW SUILLINE REMAINS FROM THE MIOCENE OF NEBRASKA.

By O. A. Peterson.

In a paper laid before the American Philosophical Society on February 17, 1888, Professor Cope proposed a new generic name for some Peccaries from the John Day formation. From his statement it appears that these Oregon forms agree in certain cranial characters with *Hyotherium* von Meyer (*Palæochœrus* Pomel) of the Miocene of Europe.

The material of this group known at present is still too imperfect, and in some cases the descriptions are too brief, to determine the validity, or non-validity, of the generic separations of *Thinohyus* Marsh[1] and *Bothrolabis* Cope.[2] From the brief descriptions and figures which Marsh gives of the two species *Thinohyus lentus* and *socialis* from the John Day, the writer infers that that genus and *Bothrolabis* are very closely related, if not the same. It is, however, best to await the discovery of more complete material, before positively expressing an opinion as to the relations between the different genera, which have been proposed by various authors. In dealing with these suilline animals, *Thinohyus* being the prior name used, I propose provisionally to treat *Bothrolabis* as a synonym.[3]

The object of the present paper is (1) to fully describe the principal characters of the porcine remains, which have been found in the Loup Fork Miocene of Nebraska by the field parties of the Carnegie Museum, working from time to time in that formation since 1901 up to the fall of the present year (1905); (2) to carefully compare the osteological characters of the new material with those already known to occur in the different species of the same genus from the John Day Miocene of Oregon; (3) it is intended, if possible, to more closely correlate and confirm the idea of Mr. Hatcher as to the relationship of these two formations.[4] By careful comparison and deduction it would seem that at least a portion of the Upper John Day is represented in the lower horizons of the Miocene sandstones of western Nebraska and eastern Wyoming.[5]

---

[1] *Amer. Jour. Sci.*, IX., p. 248, 1879.

[2] *Proc. Amer. Philos. Soc.*, Vol. XXV., p. 66, 1888.

[3] W. J. Sinclair in a recent paper (Bull. Dept. Geol., Univ. Cal., Vol. IV., p. 135, 1905), has already arrived at similar conclusions.

THINOHYUS (B.) SUBÆQUANS? Cope. (Figs. 1, 2 and 3.)

See Cope, Proc. Am. Phil. Society, Vol. XVIII., pp. 374–375, 1879; Vol. XXV., pp. 67–70, 1888.

This species is represented in the paleontological collections of the Carnegie Museum by a left mandible, No. 913. The specimen is doubtfully referred to the above species. It was found in the lowermost Nebraska beds on the Niobrara River, Sioux County, Nebraska. This horizon is undoubtedly of a much later age than the uppermost John Day of Oregon. The ramus is not in good preservation, but enough is present to determine its generic position. The following detailed description answers closely to that of *Bothrolabis trichænus*[6] Cope, but as there is no diastema back of p_2 it is well to temporarily associate the specimen with *B. subæquans.* If subsequent study of better material proves this determination to be erroneous, the name *T. brachyceps* may be substituted.

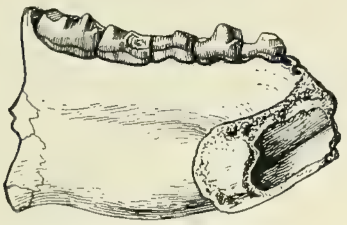
The alveolar border for the incisors is entirely wanting, as are also the canine, the first, (if there was a p_1), and second premolars. P_3 is damaged, p_4 and m_1 are complete. M_2 is slightly broken, and m_3 has lost its internal face. The angle of the jaw is broken off. The alveolus for the canine indicates a very robust tooth which corresponds perfectly to Cope's description. The alveolar border is damaged just back of the canine, so that the absence or presence of p_1 cannot be certainly determined. Cope states that this tooth in *B. subæquans* has one root, and has diastemata before and behind it, but the writer is inclined to think, in view of the considerably later age of the geological horizon in which the Nebraska specimen was found, that this tooth may in this specimen have been discarded in the process of modification. P_2 is separated from p_1 by a short diastema, and the tooth had two roots. P_3 indicates a tooth with a compressed simple crown. There is a considerable posterior heel and a slight cingulum on the antero-internal face of the tooth. P_4 has two main cusps, proto- and deuteroconids, well appressed, forming a cross-crest anterior to the middle of the crown, as in Cope's description of *Bothrolabis trichænus.* Anteriorly on this tooth there is also a small basal cusp and the cingulum on the postero-exterior angle of the tooth is thrown into a short fold forming a minute tubercle. The elevated ridge on the posterior heel, the metaconid, is perhaps more in the middle longitudinal line than, according to Cope, seems to be the case in his *Bothrolabis trichænus.* M_1 is a much worn tooth; the wear of the triturating face, however, indicates the usual quadri-tubercular style of tooth. The antero-posterior diameter is but slightly greater than that of P_4. The anterior half of m_2 is damaged internally and externally. The hypo- and entoconids are well separated on the broad grinding face, and just back of these, at the posterior border of the tooth, there is a small median cusp, the hypoconulid. In the valley between the anterior and posterior cusps is a swelling of the worn surface which indicates a small median conulid. On the internal margin opposite to this cusp is a basal pillar which fills up the bottom of the transverse valley. No other evidence of a cingulum is present on the tooth. The antero-posterior diameter of m_2 is slightly greater than that of m_1. The increase of the antero-posterior diameter of all the teeth is very gradual, as p_2 is only 5 mm. shorter than m_1. M_3 corresponds to that of *Bothrolabis trichænus* which Cope described as having "two pairs of cusps and a large heel." The paraconid can also be outlined on the tooth near the anterior cingulum. This

---

[4] *Proc. Am. Philos. Society*, Vol. XLI, p. 118, 1902.

[5] In a paper now under preparation by the writer more complete data summing up the paleontological evidence on this question will be published. (See *Annals Carnegie Museum*, Vol. III., Part 4.)

[6] *Proc. Amer. Philos. Society*, Vol., XXV., pp. 74–77, 1888.



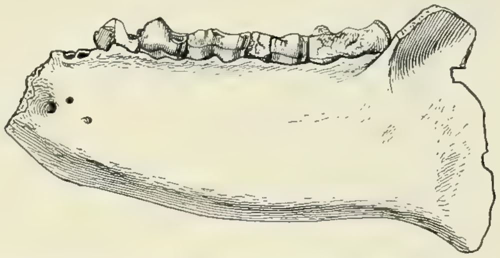


FIG. 1. Oblique internal view of left mandible of specimen No. 913, Carnegie Mus. Cat. Vert. Fossils ½ nat. size.

FIG. 2. External view of left lower mandible of specimen No. 913, Carnegie Mus. Cat. Vert. Fossils. ½ nat. size.

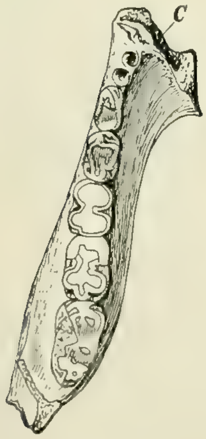


FIG. 3. Superior view of left lower mandible of specimen No. 913, Carnegie Mus. Cat. Vert. Fossils. ½ nat. size.

cingulum is interrupted on the antero-internal angle by a separate minute conulid. No other evidence of a cingulum is present on the internal side of this tooth. The external face is broken off. The enamel is slightly mammillated on the internal margin of the posterior heel; otherwise the enamel is smooth. The different tubercles of the heel are quite solidly fused together, leaving a broad triangular cross-valley back of the two posterior cusps.

The symphysis of the lower jaw is quite heavy, and indicates that the mandibular rami in this region were very broad. On the whole the ramus is rather short antero-posteriorly and deep vertically. The masseteric fossa does not extend below the line of the dentition and is indicated on the jaw fragment to be rather deep.

MEASUREMENTS.

Total length of jaw fragment		129	mm.
Depth of jaw at P_2		35	“
“ “ “ “ M_2		43	“
Length of molar-premolar series, approximately		100	“
“ “ premolar series, approximately		46	“
“ “ true molar series		54	“
Antero-posterior diameter of P_3		12	“
Diameters of P^4	antero-posterior	14	“
	transverse	10	“
“ “ M_1	antero-posterior	15	“
	transverse	11	“
“ “ M_2	antero-posterior	17	“
	transverse	13	“
“ “ M_3	antero-posterior	22	“

Thinohyus (Bothrolabis) siouxensis, n. sp.

The type of this species is based on a nearly complete skull and lower jaws (No. 1423, Carnegie Museum Catalogue of Vertebrate Fossils). The specimen was discovered by Mr. J. Grim, Jr., and was presented by him to the writer. It was found in the upper part of the Harrison horizon on the upper Niobrara River, Sioux County, Nebraska. The specific name indicates the type locality from which it came.

Some characters of the specimen might be regarded as of generic value, viz., the absence of P_1*, but it is thought best to await the discovery of more complete skeletal material before a final decision regarding its true affinities is had.

---

* The position and shape of the glenoid cavity and the posterior narial opening are similar to those in *Platygonus leptorhinus* Williston.

PRINCIPAL SPECIFIC CHARACTERS.

$I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{3}$, $M\frac{3}{3}$. *Occiput high. Region in front of the orbit elongated, with even slope of the skull, from the inion to the tip of the nasals; frontal region flat between orbits, with deep grooves leading from supraorbital foramina to very nearly the end of the nasals. The posterior margin of the orbit lies immediately in front of a line drawn vertically from the anterior border of the glenoid cavity; the infraorbital foramen is large, placed obliquely, and situated above the posterior part of* P^4. *The posterior narial orifice has an extreme posterior position.* P^1 *single-rooted and quite close to the canine, and there is a space separating it from* P^2. P^2 *is in a continuous series with the teeth back of it.* P_1 *is absent.*

CRANIUM.

The general contour of the cranium is quite similar to that of the peccary, *Dicotyles tajacu* (Linnæus), especially the region anterior to the orbits. The comparatively small size of the brain cavity, the high, sharp, and evenly sloped sagittal crest, together with the simple premolars, are characters which are striking, and at once separate this genus from the recent peccaries. The occiput is high and has a spoon-shaped excavation above the foramen magnum. The lateral occipital crest is very prominent. From the junction with the sagittal crest it descends outward and downward for a short distance, then almost vertically downward nearly to the condyle, diminishing in prominence in the latter direction, so that the surface of the exoccipital is comparatively smooth 10 mm. above the base of the occipital condyle. The posterior temporal ridge forms a weak junction with the lambdoidal crest halfway between the occipital condyle and the inion. The strong posterior temporal ridge points more strongly towards the conditions in the recent peccary and the hog than to those seen in the John Day species, according to Cope's description of the latter.

The base of the skull is injured. The occipital condyle is present, but the contact is destroyed.[7] The condyle is rather small and exhibits characters very similar to those in the peccary. There was probably a moderately large-sized foramen magnum, which separated the condyles proportionately less than in the peccary and the hog. The baso-cranial axis has a much greater angle than is seen in *Dicotyles tajacu.* This is due to the position of the posterior nares, which are relatively much farther back in *Thinohyus siouxensis* than in *Dicotyles.*

The sutures in the cranium under discussion are entirely obliterated so that the outlines of the elements cannot be traced. The basioccipital is broken posteriorly.

---

[7] The condyle is restored in its approximate position with plaster.

Anteriorly it apparently narrows rapidly, and there is a small rough tuberosity with a narrow groove through it in the median line. The basi- and presphenoids evidently have much less lateral extent than in recent genera, as the space between the tympanic regions is quite narrow. The foramina opticum and rotundum are close together; the latter is quite large. Inferiorly the sphenoids send out strong wing-shaped laminæ. These alæ are firmly joined to the squamosal at the internal base of the glenoid cavity and extend forward and downward, and obliquely outward, to again form a strong contact with the posterior part of the maxillary and the pyramidal process of the palatine. Some of the John Day species have a similar structure in this region according to Cope.[8] The region of the posterior nares of *Thinohyus siouxensis* is one of the chief characteristics of the species. The posterior exit of the orifice is between the anterior part of the tympanic bullæ, and its almost vertical direction is indicated by the large swelling on the sphenoids at the posterior boundary of the orbital fossa. In the peccary and *Platygonus leptorhinus* this orifice is located well posteriorly, but not so far back as in *Thinohyus siouxensis*.

The posterior narial border is divided anteriorly into three deep triangular grooves; one in the middle and one on either side of an osseous septum. The outside grooves are bounded externally by the deep wall of the inferior alæ of the sphenoids referred to above. The foramen ovale and lacerum anterius are located at the anterior base of the tympanic bulla and are hidden from view by the extreme forward extension of the latter. The entire occipital region of *Thinohyus siouxensis* is narrow in comparison with that of the recent peccary and the hog. The supraoccipital continues upward apparently to the top of the occiput, uniting with the parietal as in *Sus scrofa* Linnæus and *Phacochœrus æthiopicus* Linnæus. In the peccary the supraoccipital does not extend so high and is met by the downward curve of the parietal bones. The parietals in the fossil are irregularly convexo-concave. Superiorly, they terminate in the sharp sagittal crest; posteriorly they are much extended, to help form the greatly overhanging occiput. The zygomatic arch of the squamosal is very robust, especially behind. Below there is a well-formed glenoid cavity, similar to that in *Platygonus leptorhinus* and the peccary, displaying an oblique saddle-shaped surface like the glenoid cavity in some carnivora. Supero-posteriorly the arch terminates in a high, transversely broad, and thin point, with the apex gently rounded. At the base of this process (the origin of the posterior temporal ridge) on the posterior face of the arch is located the rather small external auditory meatus. Postero-laterally, the frontals show sharp and prominent temporal ridges. These ridges terminate anteriorly in the rounded and somewhat elevated superciliary border. The postorbital process is more prominent than in the recent forms and is trihedral in section. It terminates inferiorly in a sharp point somewhat posterior to the postorbital process of the jugal. The orbit is open posteriorly by a space of 12 mm. between the apices of the processes on the frontal and jugal. The posterior half of the frontals is flat and they are surrounded by the superciliary borders laterally, and by the prominent temporal ridges posteriorly. Anteriorly they gradually become convex to meet the maxillaries and nasals. The supra-orbital foramina are close together and the deep furrows which lead from them extend very nearly to the end of the muzzle.

---

[8] *Proc. Amer. Philos. Soc.*, Vol. XXV., p. 72, 1888.

The jugal has a considerable depth below the orbit. The postorbital process is strongly developed. The latter is heavy antero-superiorly and tapers gradually on the external and internal faces, forming a rather thin posterior edge. The process terminates in a subacute point. The orbit is oblique, irregularly oval, and of considerable size. On the anterior border the lachrymal tubercle divides the border into two emarginations. The one above the process is shallow, but the one below it is deeper, especially in the external face of the lachrymal. In this rounded emargination is also located the lachrymal foramen. The zygomatic arch is not so abruptly terminated at the lachrymal as in the hog, but continues in a gentle sweep forward to meet the superior border of the maxillary. The temporal fossa is proportionally much deeper than in the recent genera, while the orbital fossa is of about the same depth. The spheno-maxillary fossæ in *Thinohyus siouxensis* are extremely deep, and divided by a thin septum of bone on the median line of the cranium placed antero-posteriorly and vertically. The posterior opening of the infraorbital foramen is large. The facial region of the skull shows no sutures. The alveolar border is low, and does not extend as far back as in the peccary and the hog. The deep fossa in front and below the lachrymal which appears in *Dicotyles tajacu* is much less pronounced in *Thinohyus siouxensis.* The fossa in *Thinohyus siouxensis* is further forward. The infraorbital foramen is large, obliquely placed, and situated above the posterior part of p^4. The alveolus of the canine presents, on the external face of the maxillary, an abrupt prominent swelling. Back of this eminence is a faint horizontal ridge, which is an indication of the much stronger ridge in the recent peccary. Immediately anterior to the canine alveolus is the deep groove for the reception of the inferior canine.

The premaxillaries are heavy and greatly produced in front of the canine. The anterior palatine foramina are separated by a strong bony ridge; they are round and of considerable size. The posterior palatine foramina are close to the alveolar border and are opposite the anterior part of m_2. The palate is long and narrow, very slightly arched, and has a lightly rugose surface. There is practically no difference in the width of the palate from i^3 to back of m^3.

The tympanic region is strongly supported by the postero-internal portion of the squamosal. The tympanic bulla is of large size, filled with cancellous tissue, and is closely appressed to the postero-internal angle of the postglenoid process. Anteriorly the bulla overhangs the posterior nares in a peculiar manner, entirely hiding from view the lateral borders of the orifice. The postglenoid foramen is situated on the posterior edge of the postglenoid process, between the latter and the tympanic region. The foramen lacerum posticum and the condylar foramen are close together and are situated, the former internal to, and the latter immediately back of, the base of the paroccipital process. The foramen lacerum posticum is at the posterior boundary of the tympanic bulla.

MANDIBLE.

The lower jaws of the type are in good preservation, except the posterior part of the angle which is broken off and lost. The rami are completely coössified leaving no trace of the symphysis. The latter is long and curves evenly with the backward sweep of the horizontal ramus. The latter as a whole, is rather long and slender, diverging only slightly posteriorly, and has a short constricted area back of the canine alveole. The alveolar border is nearly horizontal back of the diastema. The latter has a considerable drop below the line of the border, causing on the external face of the ramus a constriction similar to that in *Dicotyles tajacu.* The external face of the alveolar border is reinforced by a rugose ridge extending nearly the entire length of the border. This feature is also met with in the peccary. The internal face of the horizontal ramus is slightly convex. The external surface is divided posteriorly by a prominent rounded ridge, which disappears below p_4, being replaced by a smooth surface. The inferior border of the ramus forms a sinuous line, as the angle has a considerable internal flexure. There are three mental foramina almost in a horizontal line, and situated below and in front of p_2.

The ascending ramus is strong, its anterior border, or base of the coronoid process, has a prominent ridge extending well forward on the external face of the ramus as stated above. The temporal fossa is deep; it is of considerable antero-posterior dimension, but does not extend below the line of the alveolar border of the jaw. The top of the coronoid process is broken off, but the base at the sigmoid notch indicates a rather broad antero-posterior surface. The mandibular condyle has a small antero-posterior diameter, while the transverse diameter is considerable. The coronoid process rises close to the anterior base of the condyle, forming a small superior sigmoid notch.

MEASUREMENTS.

Length of skull from occiput to end of premaxillary bone	300	mm.
“ from occipital condyle to end of premaxillary bone, approximately	260	“
“ “ lambdoidal crest to postorbital process on the frontal	91	“
“ “ postorbital process on the frontal to end of premaxillary	215	“
Total length of alveolar border including premaxillary	156	“
Length of palate from posterior narial orifice to anterior end of premaxillaries	212	“
“ “ “ “ anterior border of posterior nares to the end of the premaxillaries	160	“
Greatest transverse diameter of occiput at lambdoidal crest	44	“
“ “ “ of brain-case	49	“
“ “ “ of frontals at postorbital processes	88	“
“ “ “ of muzzle at lachrymal bone	85	“
“ “ “ at end of muzzle	34	“
“ “ “ of one condyle	21	“
Greatest diameter of cranium at tympanic region	69	“
Transverse diameter at glenoid cavity	119	“
“ “ of palate at m^3	22	“
“ “ “ “ “ p^2	22	“
“ “ “ “ “ i^3	22	“
“ “ of muzzle at canines	58	“
“ “ “ “ “ incisors	35	“
Greatest length of mandible, approximately	195	“
Length of mandible from incisor alveolar border to base of coronoid process back of m_3	148	“
Length of symphysis	53	“
Depth of ramus in front of p_2	28	“
“ “ “ back of m_3	45	“

SUPERIOR DENTITION.

PLATES XXXIV.–XXXV.

Unfortunately the incisors, canines, and premolars one and two are lacking in the type. The alveoli are all preserved and indicate a large pair of median and smaller lateral incisors; a heavy canine with the antero-posterior diameter greater than the transverse, the alveoli being oval in outline. The alveolus for p^1 is subovate, with the greatest diameter antero-posteriorly; it is close to the canine alveolus and on a line with the internal border of that tooth. P^1 was undoubtedly single-rooted. P^2 is separated from p^1 by a diastema of 5 mm. and has two roots as is indicated by the double alveolus. It had very nearly the same antero-posterior diameter as p^3. The latter tooth is firmly implanted in the maxillary by three roots. The antero-posterior diameter is a little greater than the transverse and the tooth has an oblique position. It is sub-triangular in outline with the apex antero-internal. The protocone is prominent and the posterior cingulum is modified into a broad ledge with the greatest diameter postero-internal. The tooth is entirely surrounded by a heavy cingulum. The enamel is smooth. P^4 is wider than long, as in *Thinohyus pristinus* Cope. The triturating surface of the tooth is worn down, but indicates a single external cusp, the protocone. The deuterocone is also strongly developed, and there are heavy anterior and posterior cingula. There is an external cingulum, while the tooth is smooth on its internal side.

The first and second superior true molars are much worn. The grinding surface of the former is in its worn condition a large basin surrounded by heavy enamel. The cones are entirely obliterated, but the external remnant of the transverse valley indicates a quadritubercular crown. The cingulum on the postero-external lobe is present, while that on the antero-external lobe is wanting. The internal face has no cingulum. M^2 has strong external and internal remnants of the transverse valley, extending well in on the triturating surface presenting nearly an antero-posterior 8-shaped basin. There is an anterior and posterior cingulum. Externally the cingulum is weakly developed and internally the tooth is smooth. M^2 has the greatest antero-posterior diameter of all the teeth in the upper jaw. The para- and protocones of m^3 are well worn, but indicate that they were well separated and of considerable size, especially the paracone. The meta- and hypocones are of smaller size and are closer together. The abrasion on this tooth indicates the former presence of a metaconule. The anterior half of the grinding face is too much worn to justify the statement that a protoconule was present. There is a heavy anterior cingulum and a strong posterior heel. There is no internal cingulum, while the external is faint. The tooth is broadest anteriorly and tapers rapidly on the external face from the paracone to the evenly rounded heel. The internal border is an almost straight antero-posterior line.

INFERIOR DENTITION.

PLATE XXXIV.

All the incisors of the lower jaw and also the canine on the left side are wanting. The right canine is present, but with the top broken off. This is a heavy and almost vertically placed tooth, very deeply imbedded in the mandible. Its antero-posterior diameter is greater than the transverse. There are shallow grooves on the tooth, one on the internal and one on the external face. The anterior border is narrow and evenly rounded, while the posterior border is broad and more angular, thus presenting a sub-triangular cross-section. There is a deep oblique abrasion on the posterior face caused by friction with the superior canine. P_1 is absent. There is a long diastema from the canine to p_2. The latter is in a continuous series with the teeth back of it and is implanted in the ramus by two fangs. The single protoconid is greatly developed, taking up the principal part of the crown. Antero-internally there is a minute cingular conulid ; while posteriorly the cingulum is quite strong. The external and internal cingula are wanting or only faintly indicated. P_3 has, as in p_2, only the large protoconid with the anterior cingulum heavier and the posterior heel much better developed than in the tooth in advance of it. The external cingulum is strong, and internally there is no cingulum, except on the postero-internal angle, which, together with the posterior ledge, forms a small basin on this part of the tooth. On p_4 the proto- and deuteroconids are closely fused, forming a cross-crest, which is much worn in the type. There is a strong anterior base, and the metaconid is situated almost on the middle of the posterior base. No external or internal cingula appear on this tooth. M_1 is too much worn for accurate description. There was evidently no external or internal cingulum on this tooth M_2 has the proto- and metaconids equally developed, while the paraconid is a minute element. Posteriorly the tooth is nearly as broad as anteriorly, the hypo- and entoconids being well separated. The posterior and anterior cingula are heavy. The bottom of the transverse valley is filled up externally by the cingulum ; there are no other external or internal cingula on this tooth. Molars one and two in the mandible have a quadrate appearance, while m_3 has a long sub-triangular form, which is due to the greatly extended posterior heel. The proto- and metaconids of the latter tooth are more elevated than the hypo- and entoconids. The postero-internal angle of the heel is again elevated, so as to form a broad transverse valley back of the hypo- and entoconids. The heel is solidly fused. The open transverse valley between the proto- and hypoconids is taken up medially by the hypoconulid, as is indicated by the wear on the triturating surface. There is a heavy anterior cingulum. No other cingula are present on this tooth.

MEASUREMENTS.

SUPERIOR DENTITION.

Total length of the upper dentition		155	mm.
Antero-posterior diameter of the three incisor alveoli		24	"
Diameters of the canine	antero-posterior	15	"
	transverse	10	"
Antero-posterior diameter of molar-premolar series		105	"
" " " " the premolars		53	"
Diameters of p^3	antero-posterior	14	"
	transverse	12	'
" " p^4	antero-posterior	13	"
	transverse	17	"

"	" m^1	antero-posterior	16	"
		transverse	15	"
"	" m^2	antero-posterior	1[illegible]	"
		transverse	15	"
"	" m^3	antero-posterior	18	"
		transverse	18	"

INFERIOR DENTITION.

Total length of the lower dentition			146	"
Antero-posterior diameter of incisor alveoli on one side, approximately			12	"
Diameters of canine		antero-posterior	12	"
		transverse	9	"
Diameters of	p_2	antero-posterior	11	"
		transverse	5	"
"	" p_3	antero-posterior	13	"
		transverse	7	"
"	" p_4	antero-posterior	14	"
		transverse	9	"
'	" m_1	antero-posterior	16	"
		transverse	12	"
"	" m_2	antero-posterior	18	"
		transverse	15	"
"	" m_3	antero-posterior	23	"
		transverse	14	"

In the paleontological collection of the Carnegie Museum is another specimen, No 1418, Carnegie Museum Catalogue of Vertebrate Fossils (see Fig. 4), which I refer to the same species described above. The specimen was found on the Agate Spring Stock Farm, Sioux County, Nebraska, by Harold J. Cook, Jr., and was presented by him to the writer. The specimen, having (although badly worn) incisors, a canine, and premolars in the upper jaw, and canines, and all the premolars in the lower jaw, supplements the type in important respects. Although the skull is distorted, it gives the complete length of the premaxillary and the nasals, which are damaged in the type. Anteriorly the nasals appear to be narrow, and terminate in a short subacute point, which slightly overhangs the anterior nares. In spite of the crushed condition of the skull it is possible to recognize characters like those encountered in the type of *Thinohyus siouxensis.* In No. 1418, the specimen under discussion, the excavations for the lower canines are deeper, and the anterior palatine processes of the maxillaries, immediately anterior to the canines, appear to be somewhat more constricted, than in the type. The distortion may possibly be in part the cause of this appearance.

The animal was an old individual, as is plainly indicated by the extremely worn condition of the teeth. The crown of the median incisor in its worn state has the appearance of a large, short, subcircular cylinder, with a strong curved fang deeply imbedded in the heavy premaxillary. The triturating surface is convex in all directions by wear. The external margin has received the greatest abrasion. I[2] is less worn, is much smaller than i[1], and has a basal cingulum on the postero-internal angle. I[3] is the smallest of the series. This tooth is more ovate in cross-section, the antero-posterior diameter being the greatest. The crown is surrounded by enamel which terminates posteriorly in an acute angle. There is no cingulum. The principal wear is located obliquely on the anterior half of the crown. All the incisors are divided by short diastemata. The canine of this species is very heavy, rivaling that of *Dicotyles tajacu.* In the fossil the cross-section of the tooth is a more rounded oval than in the recent genus, but, as in the latter, the posterior border is narrower than the anterior. There is a long gradual abrasion caused by friction with the inferior canine on the anterior face, which terminates in a rather blunt point, with traces of additional wear on the external face. Twelve mm. above the point of the right canine, on the external face, is a peculiar broad open abrasion, extending quite across the tooth antero-posteriorly. On the left tooth is a corresponding abrasion not nearly so well defined. These rubbed surfaces may indicate the habits of the animal, at least I cannot account for the wear, except by supposing that the canine was used for rooting. P[1] is separated from the canine by diastemata, a very short one in front and a longer one behind. This tooth is one of the chief characteristics of this species. It is a small tooth with the single pro-

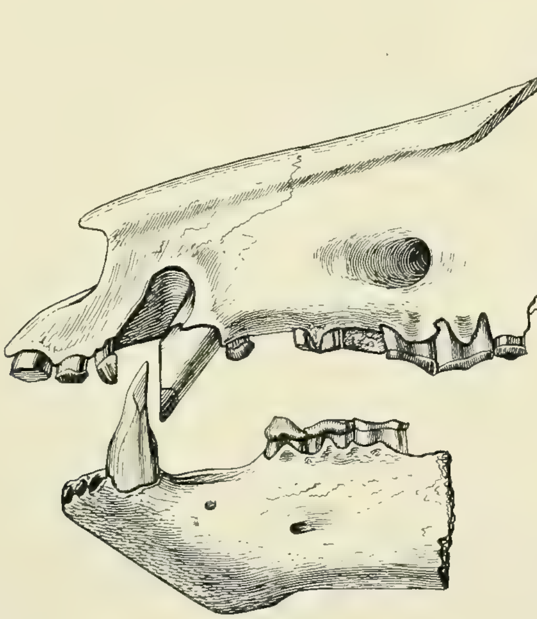


FIG. 4. Anterior portions of the upper and lower jaws of specimen No. 1418, Carnegie Mus. Cat. of Vert. Fossil. $\frac{1}{2}$ nat. size.

tocone, which has received very little wear on account of the absence of p_1. There are no cingula, except on the anterior and posterior angles on the internal side. The tooth is implanted in a single alveolus. The two roots are closely coalesced, with a groove indicating the separation of the roots in the species of earlier Tertiary times. The premolars and molars back of p^1 are so badly worn that they present no characters capable of description.

The fragment of the lower jaws which belongs to this specimen (No. 1418) indicates an animal somewhat larger than the type. The ramus is somewhat deeper and the diastema back of the canine is longer than in the type specimen. The diameters of the teeth are practically the same as in the type. The principal features of the fragment are the solidly fused chin and the absence of p_1, showing a correspondence to the type. The canine reveals a long abrasion on the antero-external angle which has removed part of the enamel, forming of the remaining enamel a diamond-shaped surface at the summit of the tooth.

MEASUREMENTS.

Length of skull from supraorbital foramen to end of premaxillaries		200	mm.
" " " " infraorbital foramen to end of premaxillaries		112	"
" " alveolar border from m^1 to end of premaxillaries		108	"
Antero-posterior diameter of the incisors		27	"
Diameters of I^1	antero-posterior	10	"
	transverse	9	"
" " I^2	antero-posterior	7	"
	transverse	6_5	"
" " I^3	antero posterior	5_5	"
	transverse	5	"
" " canine at base	antero-posterior	14	"
	transverse	10	"
" " p^1	antero-posterior	6	"
	transverse	4	"
" " c_1	antero-posterior	13	"
	transverse	10	"

DISCUSSION OF RELATIONSHIP.

It will be safest to await the discovery of more perfect material representing this group of Miocene peccaries before expressing a positive opinion as to their affinities. There are two types of the genus *Thinohyus*, a dolichocephalic and a brachycephalic. Professor Cope separated *Thinohyus decedens*, generically from other John Day forms, giving as the principal character the absence of p^2, which is found to be erroneous.[9] Judging from the description by Cope and Sinclair, and also from the illustration [10] by the latter author, it would seem that, aside from the erroneous definition of dental characters by Cope, this species is strongly characterized by its short skull and its inflated facial region, and may, when additional material is known, justify its retention in the separate genus *Chænohyus* proposed for it by the latter author.

---

[9] Sinclair, Bull. Dept. of Geol., Cal. Univ., Vol. IV., p. 135, 1905.

Thinohyus siouxensis is easily distinguished from other known species by the single-rooted p^1, which has a short diastema in front and a somewhat longer diastema behind; the unbroken sequence of p^2 with teeth back of it; the extreme posterior position of the posterior narial orifice; the large and anteriorly projecting tympanic bullæ; the posterior position of the infraorbital foramen, *i. e.*, above back part of p^4, and the absence of p_1. The skull of *T. siouxensis* is of approximately the same size as that of *T. rostratus* Cope, but the latter species differs from the former in important characters, viz., the two-rooted p^1, which is separated from the canine and p^2 by diastemata; the latter tooth also has diastemata in front and behind. The molar-premolar series is relatively shorter, and the infraorbital foramen is placed more in advance (above the middle of p^3). In *Thinohyus pristinus* Cope p_1 is small and as in *T. rostratus*, two-rooted, "the anterior root nearly reaching the posterior edge of the canine alveolus, . . . p^4 is wider than long and has but one external cusp." [11] M^3 is longer than wide, which is due to the large heel. The infraorbital foramen is located above the middle of p^3, which is another character showing similarity to *T. rostratus*. According to Sinclair *T. pristinus* is further characterized by diastemata in front and behind p_1. *T. trichænus* Cope has p^4 as long as wide, "and [the tooth] has a sub-quadrate base." [12] P^1 is small, one-rooted, and separated from p^2 by a short diastema. Premolars one and two in the mandible are each separated by diastemata in front and behind. In *Thinohyus subæquans* Cope the infraorbital foramen is nearly as far back as in *T. siouxensis*, *i. e.*, above the middle of p^4 in the former, and above the posterior part of that tooth in the latter species. *T. subæquans* is further characterized by the small two-rooted p^1, which is "almost entirely within the superior canine." [13] P^4 is wider than long, as in *T. pristinus* and *T. siouxensis*. In *T. subæquans* there are short diastemata anterior and posterior to p_1.[14] In *Thinohyus lentus* Marsh [15] "p_1 is separated from the canine and

---

[10] *L. c.*, Plate XVI.

[11] Cope, *Proc. Amer. Philos. Soc.*, Vol. XXXV., p. 73, 1888.

[12] *L. c.*, p. 75.

[13] Cope, *l. c.*, p. 69. (The tooth is located close to the postero-internal angle of the canine—O. A. P.)

[14] The lower jaw No. 913 in the Carnegie Museum Collection which is provisionally referred to this species is clearly that of a short-faced type such as *T. decedens*.

[15] *T. socialis* Marsh is imperfectly known. It is a John Day form of rather small size with mammillated posterior cingulum on m^3 (?). (See illustration, *Am. Jour. Sci.*, Vol. XLVIII., p. 271, Fig. 25, 1894).

p_2 by diastemata of respectively 8 mm. and 10 mm."[16] *Thinohyus osmonti* Sinclair is characterized by the long diastema in front of p_1, which is double-rooted and in an uninterrupted series with the teeth back of it. "P^1 is a single-crowned, double-rooted tooth, separated from the canine and p^2 by diastemata."[17] The infraorbital foramen appears from the photographic reproduction given by Sinclair to be above the posterior part of p^3.

SUMMARY.

The study of the remains described above may be summarized as follows:

1. The animals represented by the specimens in the Paleontological Collection of the Carnegie Museum are more modified than those representing the John Day Miocene in other collections, and the former may, when more completely known be regarded as new genera.

2. The horizon in which the remains were found is the upper part of the Harrison horizon, which is regarded by Hatcher[18] as filling the hiatus between the Upper and Lower Deep River Formations. The uppermost Arikaree, or the Monroe Creek horizon, which is regarded by the same author as equivalent to the Upper John Day, has not as yet yielded any remains of peccaries. When such remains are found in the lower horizons of the Miocene in this locality, they will undoubtedly reveal characters more closely allying them to the John Day forms, thus differing from *Thinohyus siouxensis.*

The writer wishes to express his thanks to Dr. W. J. Holland, Director of the Carnegie Museum, for kind suggestions and assistance in the preparation of this manuscript for the press.

The illustrations are from drawings made by Mr. Sydney Prentice.

Carnegie Museum, November 24, 1905.

---

[16] Sinclair, Bull. Dept. of Geol. Cal. Univ., Vol. IV., p. 140, 1905.

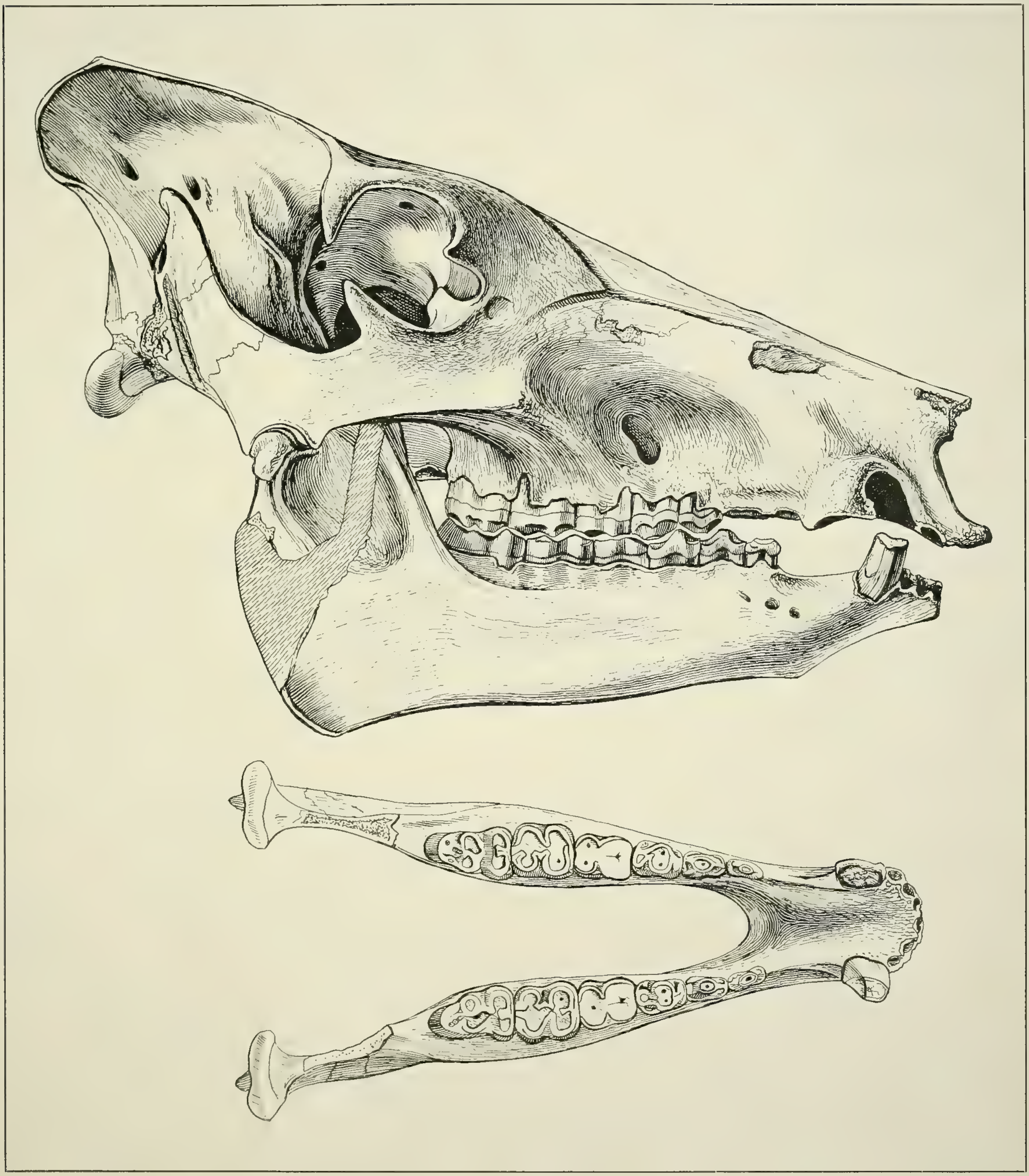
[17] Sinclair, *l. c.*, p. 139.

[18] *Proc. Amer. Philos. Soc.*, Vol. XLI., p. 118, 1902.

EXPLANATION OF PLATE XXXIV.

Upper figure. Right side of skull and lower jaws of *Thinohyus siouxensis.* (Type) No. 1423, Carnegie Museum Catalogue of Vertebrate Fossils.

Lower figure. Superior view of the mandible *Thinohyus siouxensis.* (Type) No. 1423. Figures $\frac{2}{3}$ natural size.

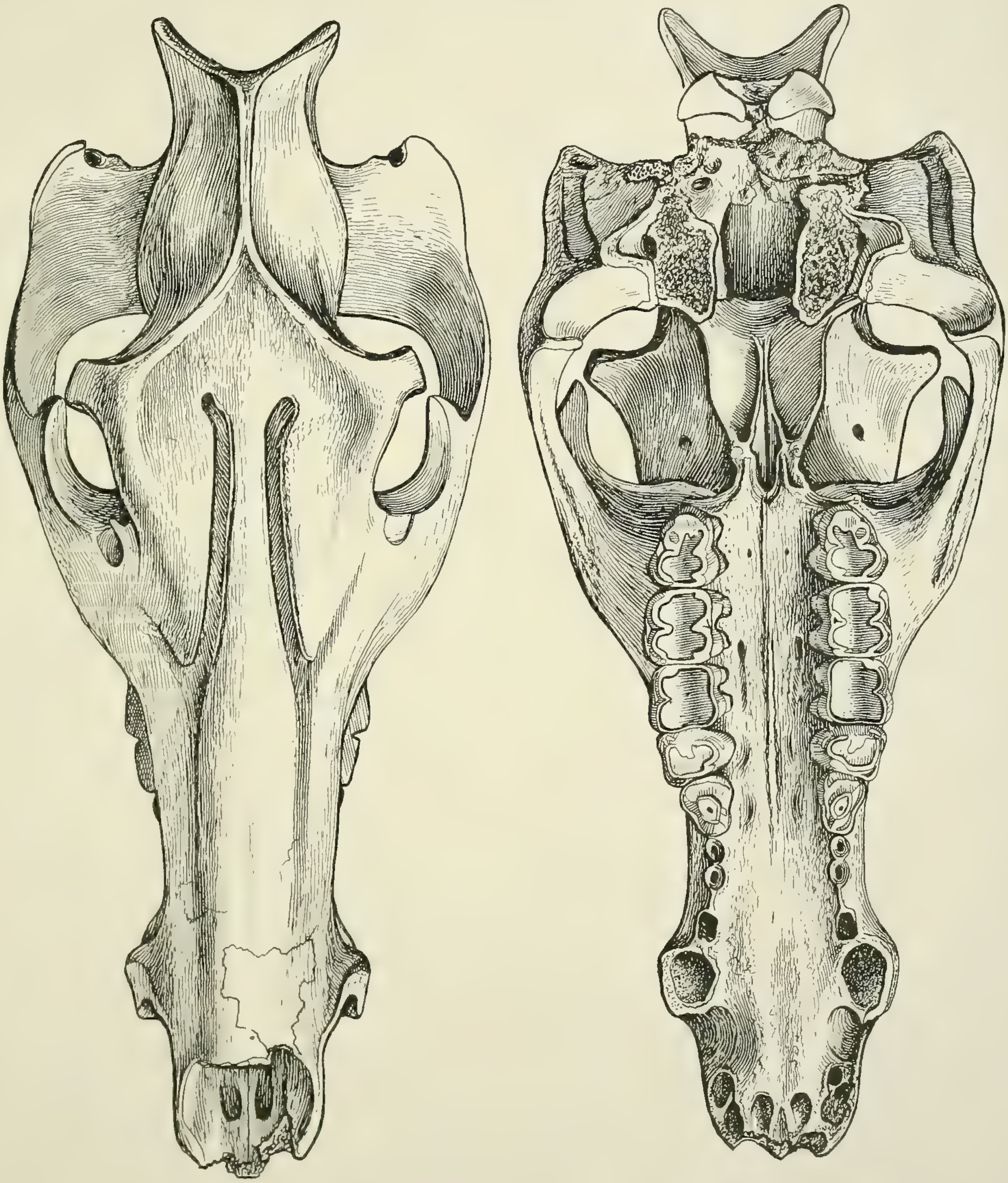


THINOHYUS SIOUXENSIS PETERSON.

EXPLANATION OF PLATE XXXV.

Figure on left. Superior view of skull of *Thinohyus siouxensis.* (Type) No. 1423, Carnegie Museum Catalogue of Vertebrate Fossils.

Figure on right. Palate view of same skull. (Type) No. 1423. Figures ⅔ natural size.



THINOHYUS SIOUXENSIS PETERSON.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 9.

NOTES ON OSTEOLOGY OF BAPTANODON.

WITH A DESCRIPTION OF A NEW SPECIES.

BY CHARLES W. GILMORE.

During the season of 1903, while in the service of the Carnegie Museum, the writer collected from the marine beds of the Jurassic in the Freeze Out Mountains in Carbon County, Wyoming, quite a complete Baptanodon skull (No. 1441[1]) and lower jaws associated with other parts of the skeleton.

Through the courtesy of the Director, Dr. W. J. Holland,[2] the writer was accorded the privilege of studying this specimen, thinking perhaps it would give some information regarding the obscure points in our knowledge of the anatomy of this interesting reptile.

The skeleton like nearly all of the American Jurassic Ichthyosaurians was enclosed in a very hard limestone concretion[3] much seamed and cracked by exposure to the elements.

Since publishing a paper on the Osteology of Baptanodon[4] additional discoveries have thrown new light on the structure of this animal. It thus becomes necessary to make certain alterations and additions to the description and drawings then given, especially those relating to the elements of the skull and lower jaws.

---

[1] Card catalogue number, Department of Vertebrate Fossils of the Carnegie Museum.

[2] My acknowledgments are especially due Dr. W. J. Holland, and I take this opportunity to express my appreciation of the many courtesies extended during the preparation of these notes. The text-figures were drawn by Mr. H. W. Hendley, of the U. S. National Museum, Washington, D. C.

[3] A recent letter from W. H. Reed, of the Museum of the University of Wyoming, informs me that during the past summer he collected a very complete Ichthyosaurian skeleton, which was quite free from the refractory matrix mentioned above. He regards this specimen as coming from a lower horizon than those found in the concretionary layer.

[4] MEMOIRS OF THE CARNEGIE MUSEUM, Vol. II., No. 2, August, 1905.

The parts of specimen No. 1441 recovered consist of a skull and lower jaws lacking a median section of the rostrum, the coössified atlas and axis, third and fourth cervicals, besides vertebræ in various stages of preservation from other parts of the vertebral column. With the exception of the proximal end of one humerus, the ulna, and a few paddle bones, all other elements are missing.

The Skull.

The cranium, although subjected to severe pressure, which has somewhat distorted the outlines of the skull, appears very similar to those previously described in the paper above mentioned, with the exception that it pertains to a somewhat smaller individual.

The superior view shows the transverse displacement between the anterior end of the postfrontal and the posterior end of the nasal, and, as breaks occur in identically the same place, and take the same transverse direction in two other crania (Nos. 603 and 878) in the collections of the Carnegie Museum, the writer now assumes this displacement as following the line of suture, and in the corrected drawing (See Plate XXXVII., Fig. 1), they are indicated as absolutely determined. The suture separating the premaxillæ at the anterior third of the rostrum is plainly shown in this specimen. Another point of interest is the wide prefrontal developed in this individual.

Viewed laterally this skull sheds new light on the posterior termination of the premaxillary. In *Baptanodon* the posterior end of the premaxillary is somewhat forked as in many forms of the Ichthyosauria. The lower posterior branch extends back under the nares, laps over and hides from a lateral view most of the anterior prolongation of the maxillary. (See Plate XXXVI.) The longitudinal channel along the side of both the premaxillaries and dentaries, just above and below the dental grooves (See Fig. 3), has many more nerve pits for the entrance of nerves to the teeth than was indicated in the first restoration of the skull of *Baptanodon*. A pineal foramen appears to be present and occupying essentially the same position as in the other skulls in this museum. The posterior part of the skull is so badly disarranged that nothing of importance is shown.

The other views of the skull show nothing new, and, as the other elements have been fully described in a previous paper, it is unnecessary to repeat the description here.

Lower Jaws.

A study of the well preserved jaws of No. 1441, not only shows the exact number of elements composing the mandible as six pairs of bones; but it also indicates clearly the extent and relative positions of these elements, particularly those bones composing the posterior portion of the rami, which previous to the discovery of this specimen had not been well understood.

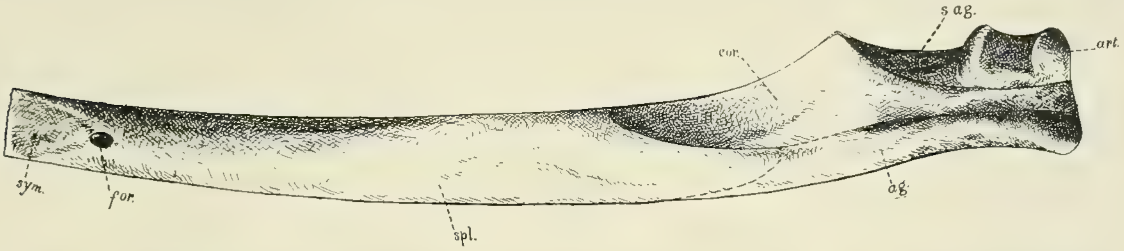


Fig. 1. Internal view of the right mandibular ramus of *Baptanodon natans* (No. 1441). One fourth natural size. *art.*, articular; *ag.*, angular; *cor.*, coronoid; *for.*, foramen; *s.ag.*, surangular; *spl.*, splenial; *sym.*, beginning of the symphysis.

This specimen (No. 1441) gives the first positive knowledge of the shape and extent of the coronoid in *Baptanodon.* Figs. 1 and 2 show it to be a thin plate of bone extending along the inner side of the posterior end of the ramus. Its lower border laps along the upper internal border of the angular except anteriorly where it overlaps the posterior prolongation of the splenial. The anterior termination is somewhat in advance of the node-like protuberance developed upon the upper border of the surangular, where it is overlapped by the posterior end of the splenial. Posteriorly the coronoid is narrow, and laps along the articular, thus assisting the surangular in holding that element in position. More anteriorly the coronoid widens rapidly, the upper margin being elevated in a dorsal process which is nearly the height of the protuberance on the surangular. Anterior to this process it gradually narrows to the point where it meets the overlapping splenial. The posterior end of the splenial is wholly confined to the internal side of the ramus. The exact extent of the lower posterior prolongation could not be determined from this specimen. The splenials enter the symphysis and entirely separate the dentaries posteriorly.

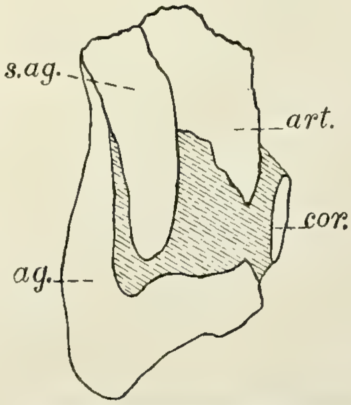


Fig. 2. Cross-section of posterior end of left mandibular ramus of *Baptanodon natans* (No. 1441). Natural size. *art.*, articular; *ag.*, angular; *cor.*, coronoid; *s.ag.*, surangular.

The anterior part of the splenial has been fully described in a previous paper. The oval foramen present in the jaws of No. 603 (*loc. cit.*, p. 96) is also present near the symphysis in this individual. (See *for.*, Fig. 1.) The suture between the surangular and angular on the external posterior end of the ramus now appears to be accurately determined, as following nearly the course provisionally indicated in the first restoration of the skull and jaws. (See Plate XXXVI.)

Fig. 2 shows how the angular laps over and along the surangular, although the two elements were probably more closely applied than is shown by the cross-section.

The articular appears very similar to those described previously, though perhaps more robust and occupying a more nearly horizontal position in the ramus.

The rami are very slender for their length and height.

MEASUREMENTS.

No. 1441.	Greatest length of coronoid, about	220 mm.
" 1441.	" width " " "	45 "
" 1441.	" " " posterior end of ramus	70 "
" 1441.	" " " anterior " " "	18 "

THYROHYAL.

This specimen, as in No. 878 in the collections of the museum, has the right thyrohyal preserved quite intact. It was retained in the matrix parallel to the inner posterior part of the ramus of that side. The anterior extremity while somewhat expanded is more circular in cross-section than was indicated by the element mentioned above. There is evidence of the opposite element in a fragmentary posterior end found in the matrix along the other ramus. Otherwise the shape and proportions are very similar to the thyrohyal of No. 878 described and figured previously.

SCLEROTIC PLATES.

Although crushing has badly distorted the sclerotic rings of both orbits there appears to be essentially the same number of plates (14) as observed in other members of this genus. The distortion mentioned above has so displaced the plates that the manner in which they overlap one another is clearly shown. (See Fig. 3.)

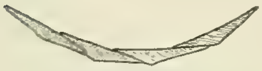


FIG. 3. Cross-section of sclerotic plates of *Baptanodon natans* (No. 1441). One half natural size.

The plates lap over one another from left to right, the bevelled edge of one over-lapping the reverse bevel of the other. This long free union of the plates would allow the sclerotic ring to expand and contract considerably. One orbit shows the bony covering extending back 40 mm. from the periphery, and it appears quite probable that this covering extended to the very back of the eyeball as in some birds. It may prove to be the case that these bony plates curve in on the back of the eye similar to the cartilaginous protection of the eyes in some of the whales. The surface markings of the sclerotic plates have been fully described in a previous paper.

Dentition.

No. 1441 gives but little information regarding the teeth of this form. Only one tooth was found intact, this being in position near the anterior end of the rostrum. (See Fig. 4.)

This tooth measures 13 mm. in length and is a good example of the anterior teeth as known in two other individuals of this group. There is no swelling at the base, as may be observed in the teeth of some of the Ichthyosaurs. This tooth is circular in cross-section, ending in a sub-acute apex, the top being covered with enamel without striation. In the latter respect the tooth appears very similar to the single tooth known in the type of *Baptanodon natans*. There are parts of other teeth preserved which are more slender and pointed than the one just described, but their enameled surfaces are perfectly smooth. The presence posteriorly of faint alveolar partitions indicates the position of other teeth. Because of the small size of this individual and the apparent similarity of the teeth I refer this specimen to *B. natans*. Fig. 5 shows a cross-section of the rostrum somewhat anterior to the symphysis and gives a good idea of the depth and shape of the dental grooves in this part of the snout.

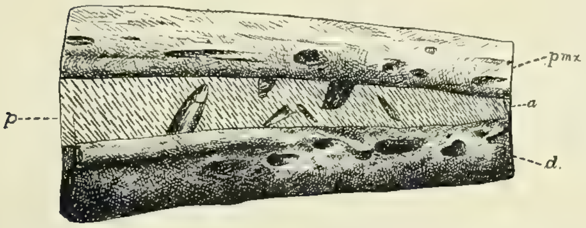


Fig. 4. Lateral view of a section of the anterior part of the rostrum of *Baptanodon natans* (No. 1441). One half natural size. *a.*, anterior end; *d.*, dentary; *p.*, posterior end; *pmx.*, premaxillary.

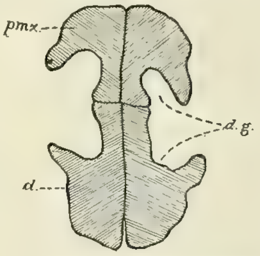


Fig. 5. Cross-section near the middle of the snout of *Baptanodon natans* (No. 1441). One half natural size. *d.*, dentary; *d.g.*, dental grooves; *pmx.*, premaxillary.

Vertebræ.[5]

The atlas, axis, third, and fourth cervicals were found in the matrix but little removed from their normal position at the back of the skull and still in contact with the basioccipital. These elements are smaller than the homologous parts of *B. marshi* and *B. discus* and are hardly more than half the size of *B. robustus.* They differ in several minor characteristics. The atlas resembles *B. marshi* and *B. robustus* in having a single hypapophysis on the lower anterior surface of the centrum. The third and fourth cervicals differ from the same elements of *B. marshi* in having well developed parapophyses, and very small diapophyses.

---

[5] Mr. W. H. Reed writes me that there are fifty consecutive vertebræ in the caudal series of specimen "T" in the collection of the University of Wyoming, instead of forty-six as published by Knight and quoted by me in a later paper.

There is no indication of the parapophysis on the axis as found in both *B. marshi* and *B. discus.* Just below the diapophysis and separated from it by a non-articular tract is a faint antero-posterior ridge, which anteriorly probably represents the rudimentary parapophysis of the atlas. Midway between this ridge and the lower border is a small vertical eminence not observed in the other species. The upper arches of these vertebræ are not sufficiently well preserved to be described here. The other vertebræ preserved appear very similar to the corresponding elements in the other members of this group.

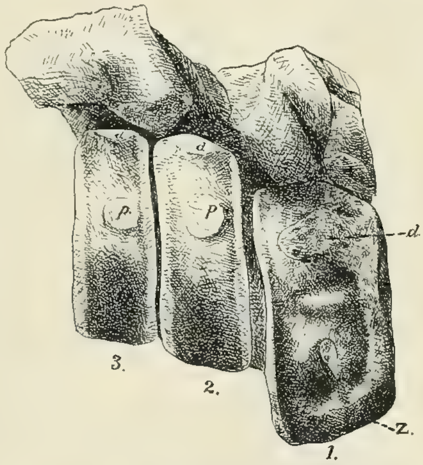


FIG. 6. Atlas, axis, third, and fourth cervical vertebræ of *Baptanodon natans* (No. 1441). One half natural size. 1. Coalesced atlas and axis. 2 and 3. Third and fourth cervicals. *d.*, diapophysis; *p.*, parapophysis; *z.*, hypapophysis.

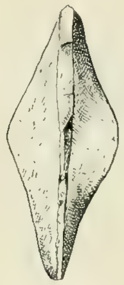


FIG. 7. Lateral view of intervertebral disk of *Baptanodon* (No. 1441). One half natural size

Intervertebral Disks.— Fig. 7 represents the shape and size of the matrix filling the space between the centra of the anterior vertebræ. These biconvex disks are quite uniform in character and give an accurate idea of the thickness of the cartilage that once filled the spaces between the centra. The average thickness of the disks at their middle is about 30 mm.

Anterior Limbs. — About half of the proximal portion of one humerus was found. Fig. 8 shows the subrectangular outline of this articular end. The surface of this end is somewhat weathered and worn, and does not show the very rugose nature observed in better preserved specimens. The head is very convex, the portion for cartilaginous attachment extending far around both anteriorly and posteriorly. There is a well developed trochanter on the dorsal surface.

The *ulna* is a pentagonal block of bone, the proximal being thicker than the distal end. The proximal end is slightly convex and was opposed to the concave facet on the distal end of the humerus though probably separated by cartilage. The other sides are slightly convex and were evidently surrounded by a thick cartilage as indicated by their rugose surfaces. The upper and lower surfaces are slightly concave antero-posteriorly. The element appears to be more angular than the ulna of *Baptanodon marshi.*

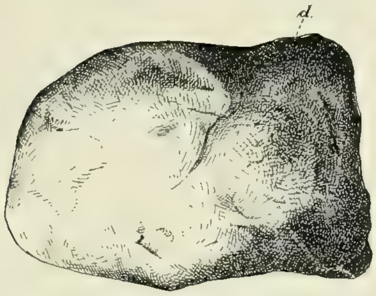


FIG. 8. View of the proximal end of the humerus of *Baptanodon natans* (No. 1441). One half natural size. *d.*, dorsal surface.

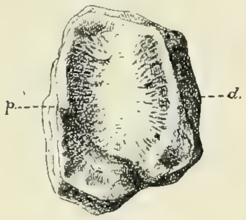


FIG. 9. Ulna of *Baptanodon natans* (No. 1441). One half natural size. *d.*, distal end; *p.*, proximal end.

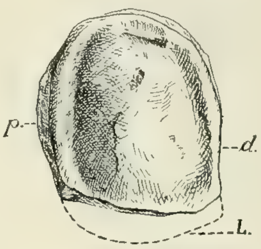


FIG. 10. Radius of *Baptanodon natans* (No. 1441). One half natural size. *d.*, distal end; *l.*, lateral border, restored; *p*, proximal end.

MEASUREMENTS.

No. 1441.	Greatest length of ulna antero-posteriorly	40 mm.
" 1441.	" breadth of ulna	50 "
" 1441.	" thickness of ulna, proximal end	35 "
" 1441.	" " " distal "	25 "

The *radius* is a sub-quadrate element somewhat wider than long and like the ulna thicker on the proximal than on the distal end. The external margin is missing but apparently reduced to a comparatively thin edge. The radius is larger than the ulna in all of its dimensions. The proximal end is convex and was opposed to the largest of the three concave facets on the distal end of the humerus. The inner side is slightly convex, the distal flat, and all except the external side are rugose. The upper and lower surfaces are slightly concave antero-posteriorly.

MEASUREMENTS.

No. 1441.	Greatest length of radius antero-posteriorly, estimated	51 mm.
" 1441.	" breadth of radius	65 "
" 1441.	" thickness of radius, proximal end	42 "
" 1441.	" " " distal "	30 "

Pelvic Element.

With specimen 603 in the collection of the Carnegie Museum is a portion of a bone which at the time of preparing my memoir on *Baptanodon* I was unable to identify but since have concluded that it represents the acetabular end of the ilium. This end is expanded into a thickened head somewhat roughened on the acetabular surface. The shaft above the head is constricted up to the fractured end, both antero-posteriorly and internally. One side of the bone is flattened and probably represents the internal surface. The fractured end is nearly half oval in cross-section. (See (3), Fig. 11.) If correctly determined this is the first evidence we have of the character of the pelvic region in *Baptanodon* and it appears to indicate a weak posterior extremity as compared with the strong anterior limb. It also furnishes additional evidence that Professor Marsh was mistaken in his identification of the limb in the type of *B. discus* (1955)[6] as a posterior extremity, a question discussed in my previous paper. This element resembles somewhat the ilium of *Toretocnemus californicus*, a Triassic Ichthyosaurian described by Dr. J. C. Merriam.

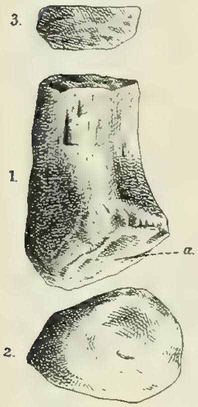


Fig. 11. (1), external view of the acetabular end of the ilium of *Baptanodon discus* (No. 603), one half natural size, *a.*, articular end; (2), view of articular end of same; (3), cross section of the broken end.

Measurements.

No. 603.	Greatest width antero-posteriorly of acetabular end	45 mm.
" 603.	" " " " fractured end	27 mm.

Baptanodon robustus sp. nov.

The type material of this species includes a fairly well-preserved pectoral girdle, a series of ten cervical vertebræ beginning with the atlas; a second series of eleven vertebræ from the anterior dorsal region commencing back of the point where the diapophysis becomes distinct from the neurapophysial articular surface; a third section of eleven posterior dorsals beginning just back of the first vertebræ having the diapophysis and parapophysis united to form a single node-like articulation for the single headed ribs of this region. The fourth and last section contains parts of twelve anterior caudals. These show the rapid decrease posteriorly in the size of the centra, which has been previously pointed out by Knight.[7]

This specimen, No. 919, is from the Red Fork of Powder River, Big Horn County,

---

[6] Catalogue number of Museum of Yale University.

[7] Knight, W. C., "Some Notes on the Genus Baptanodon with Description of a New Species," *Amer. Jour. of Science* (4), Vol. XV., 1903.

Wyoming, and was collected by Mr. W. H. Utterback from the marine beds of the Jurassic in 1902. It is now in the collection of the Carnegie Museum.

The large size of all of the vertebræ and the long straight border of the external ends of the coracoids for articulation with the humeri appear to indicate a new species for which I propose the name *Baptanodon robustus.* Although the material at hand is insufficient for a satisfactory diagnosis of this form, yet the dimensions of the parts preserved, particularly the vertebræ and ribs, show this to be the largest member of the *Baptanodontidæ.* A right coracoid, No. 1953, in the Museum of Yale University shows the same long straight border on the external end and may pertain to this species.

Vertebræ. — The coalesced atlas and axis are very large, and this is the first individual I have examined which shows the suture separating these vertebræ. (See Fig. 12, *S.*) On the lower border the atlas is 35 mm. wide antero-posteriorly, the axis being 30 mm. The great disparity in length antero-posteriorly between the lower and upper parts of the combined centra appears to be distinctive of this species. The hypapophyses on these vertebræ are very indistinct and no attempt has been made to indicate them in the drawing. (See Fig. 12.)

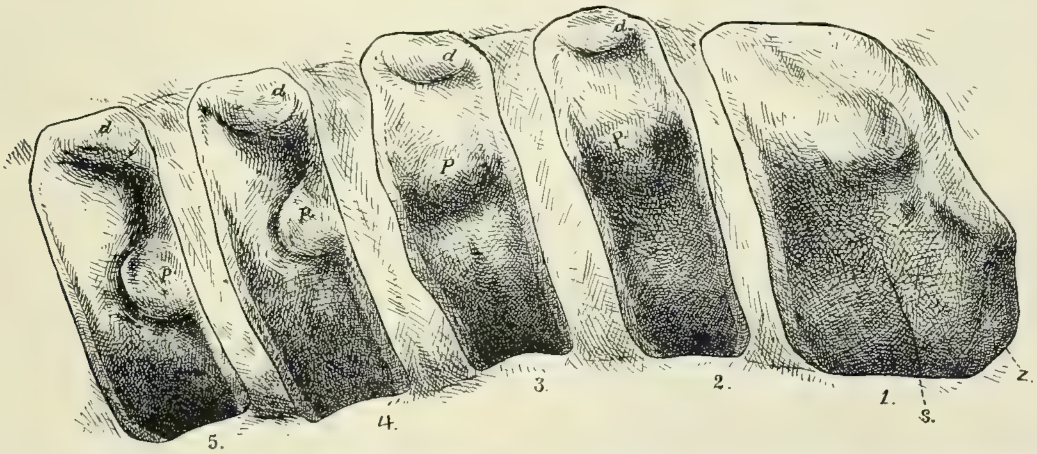


FIG. 12. Atlas, axis, third, fourth, fifth, and sixth cervical vertebræ of *Baptanodon robustus.* Type specimen, No. 919. One half natural size. 1, Coalesced atlas and axis. 2, 3, 4, and 5, third, fourth, fifth, and sixth cervicals *d.*, diapophysis; *p.*, parapophysis; *s.*, suture between the atlas and axis; *z.*, hypapophysis.

On the third and fourth cervicals the parapophysis appears to be indicated by hardly more than a slight antero-posterior swelling on the side of the centra. In this respect it resembles somewhat the corresponding elements of *B. marshi.* The succeeding vertebræ have well developed parapophyses on the anterior half of the centra. The diapophyses on all of the vertebræ preserved are very robust and confluent with the articular surfaces on the dorsal surfaces of the centra. The fourth to the ninth cervicals have a vertical ridge connecting the di- and parapophyses on the anterior margin of the centra. This character may also prove to be a feature of this species.

The anterior or median dorsals have two well defined apophyses (See Fig. 13) placed well down on the anterior margins of the centra. The diapophysis is the larger of the two. In these vertebræ the pedicels of the upper arches are extended antero-posteriorly, being nearly as wide as the centra upon which they rest. The spines are somewhat compressed laterally, and very high. The arches in what is considered the anterior dorsal region are held together by single zygapophyses, which are of considerable extent obliquely. The pedicels do not project laterally as in some of the Ichthyopterygians but form a smooth surface with the upper lateral surfaces of the centra.

The series of posterior dorsals appear very similar, except in size, to those from this region of *B. discus*. The single apophyses posteriorly recede to the lowermost border of the centra as in the other species.

The parts of caudals preserved, besides showing the rapid decrease in size posteriorly, appear to have parts of several chevrons retained in the matrix near them and furnish the first evidence of these bones in *Baptanodon*.

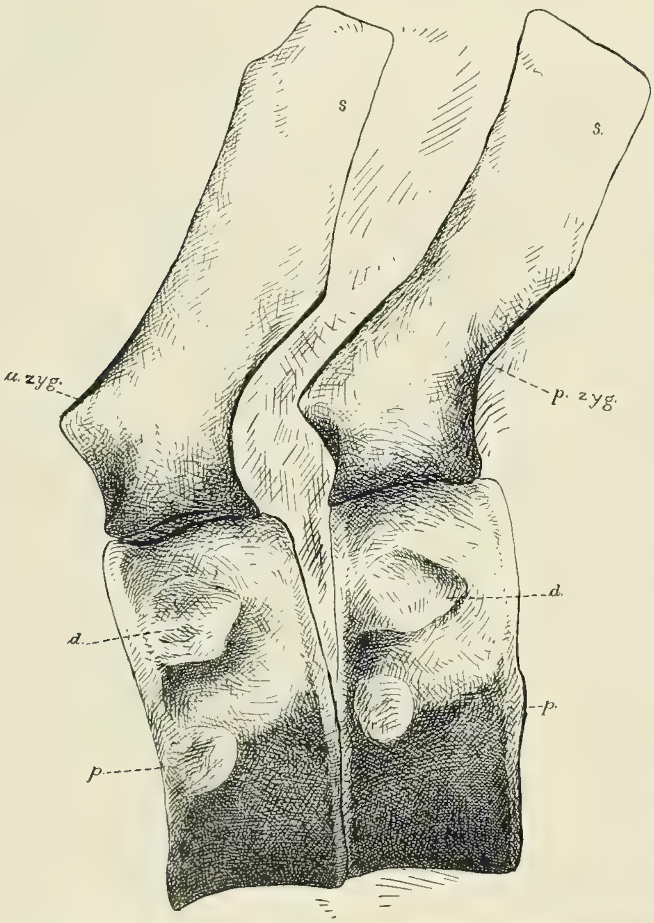


FIG. 13. Lateral view of anterior or median dorsals of *Baptanodon robustus* (No. 919). Type specimen. One half natural size. *d.*, diapophysis; *p.*, parapophysis; *s.*, spinous process; *a.zyg.*, anterior zygapophysis; *p.zyg.*, posterior zygapophysis.

All of the vertebræ are deeply biconcave as in other members of the genus.

Measurements of Vertebræ of No. 919.

Cervicals	Atlas and axis	3d	4th	5th	6th	7th	8th	9th	10th	11th	
Greatest length of centrum in mm.	57	34	34	30	35	35	35	35	*b*	—	—
Greatest width of centrum in mm.	100	100	100	90	80	70	60	60	—	—	—
Anterior dorsals	1	2	3	4	5	6	7	8	9	10	11
Greatest length of centrum in mm.	—	45	45	45	43	43	43 *a*	43 *a*	43 *a*	42 *a*	—
Greatest height of centrum in mm.	100 *b*	120 *b*	110	110 *b*	110	110	101	—	—	—	—
Greatest height with spine in mm.	210 *b*	245 *a*	245 *a*	210 *b*	—	—	—	—	—	—	—
Posterior dorsals	1	2	3	4	5	6	7	8	9	10	11
Greatest length of centrum in mm.	37	37	38	40	40	43	45	45	50	48	50
Greatest height of centrum in mm.	100	104	104	104	104	106	106	102	99	99	99

a = approximate, *b* = broken.

The Pectoral Girdle.

The elements of the pectoral girdle of No. 919 are finely preserved and entirely free from distortion. The scapulæ lack about half of their upper free ends and the coracoids their posterior borders. (See Plate XXXVIII.) These missing parts have been restored from the pectoral girdle of *B. discus*, No. 878 in the Carnegie Museum.

The *coracoids* are broad subquadrangular bones which join one another medially by large elliptical facets. The superior surfaces (Plate XXXVIII., Fig. 2) are flattened, although both elements are gently inclined toward the median line. The inferior surfaces are concave transversely and convex antero-posteriorly. The lateral borders are especially thickened forming a heavy articular face for the scapulæ and humeri. This outer articular end is divided into two unequal faces meeting in an obtuse angle. The more anterior and smaller one of the two is for the scapula, and looks outward, forward, and obliquely upward. The larger and posterior surface forms the greater part of the glenoid cavity. This border is much straighter and longer antero-posteriorly than on the coracoids of *B. discus*. It is very slightly convex from above downward and is covered with tubercle-like eminences. This articular end is supported by a broad neck formed by a deep notch on the anterior margin. The anterior border from the inner notch thickens rapidly as it recedes posteriorly to form the intercoracoidal facet. (See Plate XXXVIII., Fig. 1.)

The *scapulæ* are moderately long bones the upper halves being narrow with nearly parallel sides, the articular end is broadly expanded antero-posteriorly and thickened on their posterior margins where they enter into the formation of the glenoid cavity. The articulating face for the coracoid joins this border at an obtuse angle.

The scapulæ extend outward, upward, and forward. Viewed longitudinally the inner surface is slightly concave as they curve up to lap over the side of the ribs. The articular ends on the dorsal surfaces are concave antero-posteriorly.

The anterior border of the parts preserved is slightly rounded, but, as it approaches the articular end it widens into flattened oblique surfaces which look forward and upward and probably represent the points of attachment for the ligaments which held the clavicles in position. (See Pl. XXXVIII., Fig. 1.) The ventral surface of the scapulæ antero-posteriorly at the expanded articular ends is somewhat concave. Between the point of attachment for the clavicle and the articulation with the coracoid the internal border is especially compressed and remains free.

The clavicles and interclavicular bones were not found with this specimen.

MEASUREMENTS.

No. 919.	Greatest	width of coracoids, transversely	430	mm.
" 919.	"	length of articular surface for scapula	85	"
" 919.	"	" of straight external border	110	"
" 919.	"	width of scapulæ, antero-posteriorly	175	"
" 919.	"	length of glenoid articular face	60	"

COMMENTS ON RECENT LITERATURE.

In discussing the age of the Baptanodon Beds Dr. S. W. Williston[8] speaks of the relationship of *Baptanodon* and *Ophthalmosaurus* and makes the statement that the two species of *Ophthalmosaurus* are probably not congeneric and "it is also apparently quite true that *Baptanodon* seems to be as closely allied to the Cretaceous as to the Jurassic species." In a previous paper[9] I have shown that *O. icenicus* (the Jurassic form) and *Baptanodon* are very closely allied, while *O. cantabrigiensis* is not similar in any respect.

The discovery the past season (1905) by Mr. W. H. Reed of an Ichthyosaurian in the Benton Cretaceous is of considerable interest as showing the occurrence in North America of this group at a much later period than hitherto supposed.

Dr. J. C. Merriam, who has examined the fragmentary specimen collected by Reed, says:[10] "The centrum is very thin antero-posteriorly and in this respect somewhat resembles the corresponding centra in *Baptanodon discus*. . . . When more material is available it will be interesting to learn whether this form really represents a true *Ichthyosaurus* or possibly a more highly specialized form of *Baptanodon* than those we know from the Baptanodon beds. Should it be *Baptanodon*, it will probably show some extreme specializations, as the time separating the Benton from the Baptanodon beds is considerable."

---

[8] Williston, S. W., "Hallopus, Baptanodon and Atlantosaurus Beds of Marsh," *Jour. of Geology*, Vol. XIII., No. 4, May–June, 1905.

[9] Gilmore, C. W., "Osteology of Baptanodon," MEMOIRS OF THE CARNEGIE MUSEUM, Vol. II., No. 2, August, 1905.

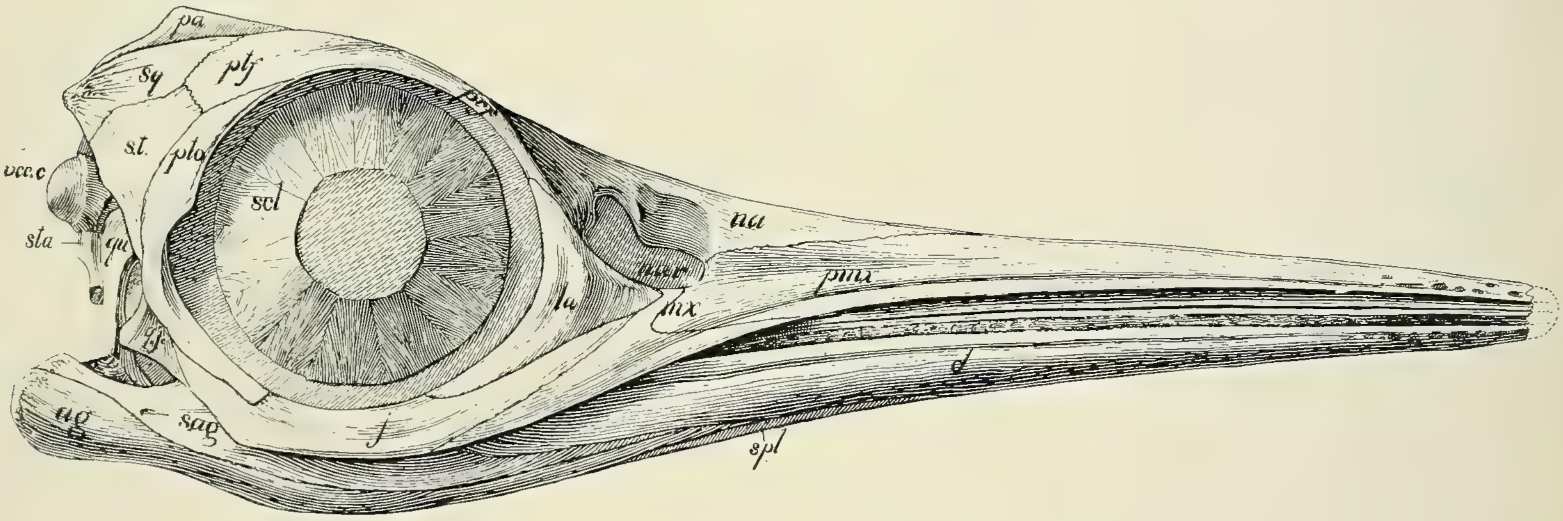
[10] Merriam, J. C., "The Occurrence of Ichthyosaur-like Remains in the Upper Cretaceous of Wyoming," *Science*, N. S., Vol. XXII., No. 568, pp. 640–641, November 17, 1905.

Moreover, it would be of interest to note the presence of this group in the Cretaceous of this country, which has already been shown to be the geological range of the closely allied European genus *Ophthalmosaurus*.

U. S. National Museum,
February 6, 1906.

EXPLANATION OF PLATE XXXVI.

Side view of skull of *Baptanodon discus* Marsh (No. 878). One fifth natural size. Restored. *ag.*, angular; *d.*, dentary; *j.*, jugal; *la.*, lachrymal; *mx.*, maxillary; *na.*, nasal; *nar.*, narial opening; *occ.c.*, occipital condyle; *pa.*, parietal; *pmx.*, premaxillary; *prf.*, prefrontal; *ptf.*, postfrontal; *pto.*, postorbital; *q.j.*, quadrato-jugal; *qu.*, quadrate; *s.ag.*, surangular; *s.t.*, supratemporal; *scl.*, sclerotic plates; *sta.*, stapes; *spl.*, splenial; *sq.*, squamosal.

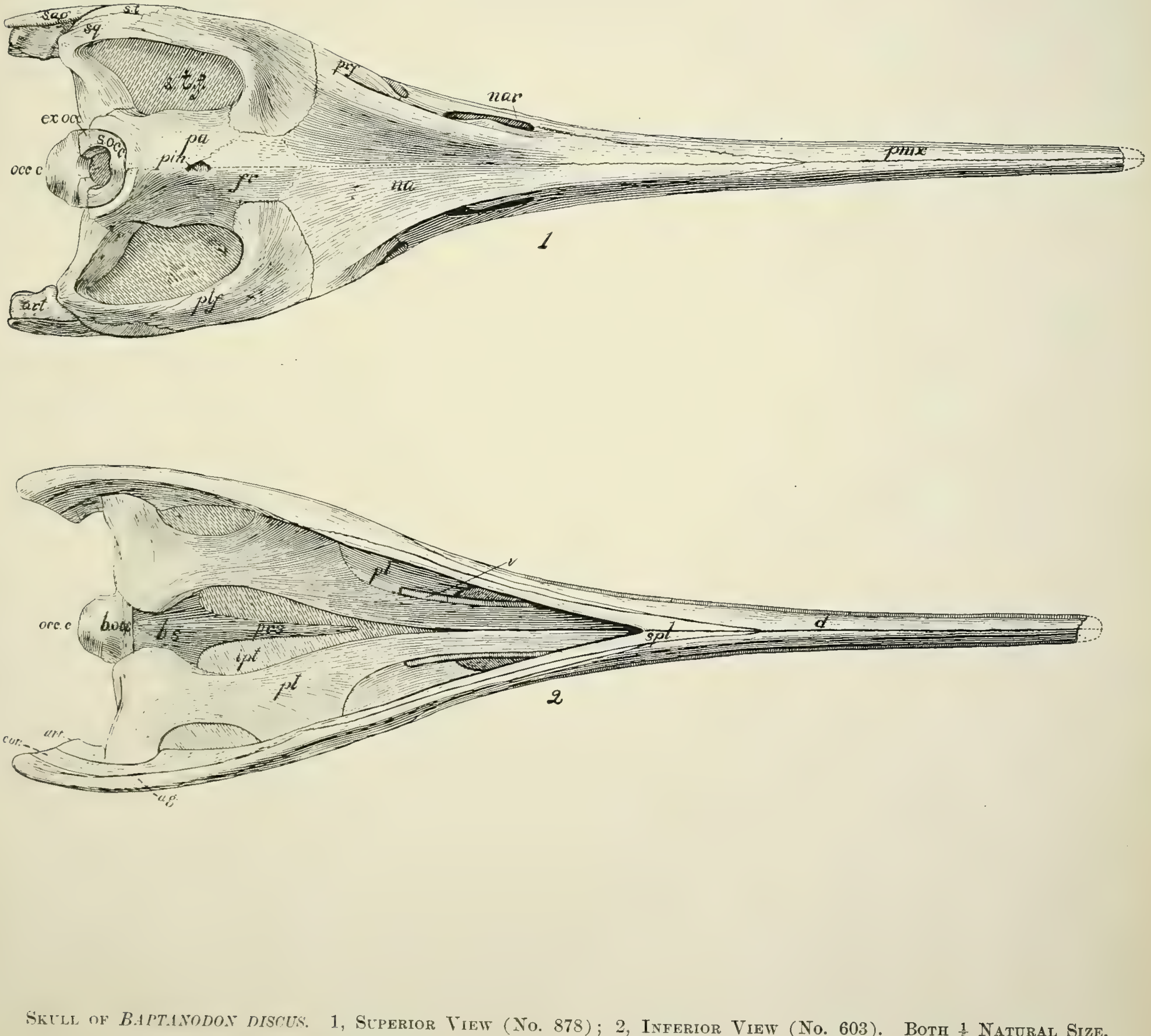


SIDE VIEW OF SKULL OF *BAPTANODON DISCUS* MARSH (No. 878). $\frac{1}{5}$ NATURAL SIZE. RESTORED.
SOME SUTURES DRAWN AFTER No. 1441.

EXPLANATION OF PLATE XXXVII.

1. Top view of skull of *Baptanodon discus* Marsh (No. 878). One fifth natural size. Restored. *art.*, articular ; *ex.occ.*, exoccipital ; *fr.*, frontal ; *na.*, nasal ; *nar.*, nares ; *occ.c.*, occipital condyle ; *pa.*, parietal ; *pin.*, pineal foramen ; *pmx.*, premaxilla ; *prf.*, prefrontal ; *ptf.*, postfrontal ; *s.ag.*, surangular ; *s.occ.*, supraoccipital ; *s.t.*, supratemporal ; *s.t.f.*, supratemporal fossa ; *sq.*, squamosal.

2. Inferior view of skull of *Baptanodon discus* (No. 603). One fifth natural size. Restored. *ag.*, angular ; *art.*, articular ; *b.occ.*, basioccipital ; *b.s.*, basisphenoid ; *cor.*, coronoid ; *d.*, dentary ; *ipt.*, interpterygoid vacuity ; *occ.c.*, occipital condyle ; *pl.*, palatine ; *prs.*, presphenoid ; *pt.*, pterygoid ; *spl.*, splenial ; *v.*, vomer.

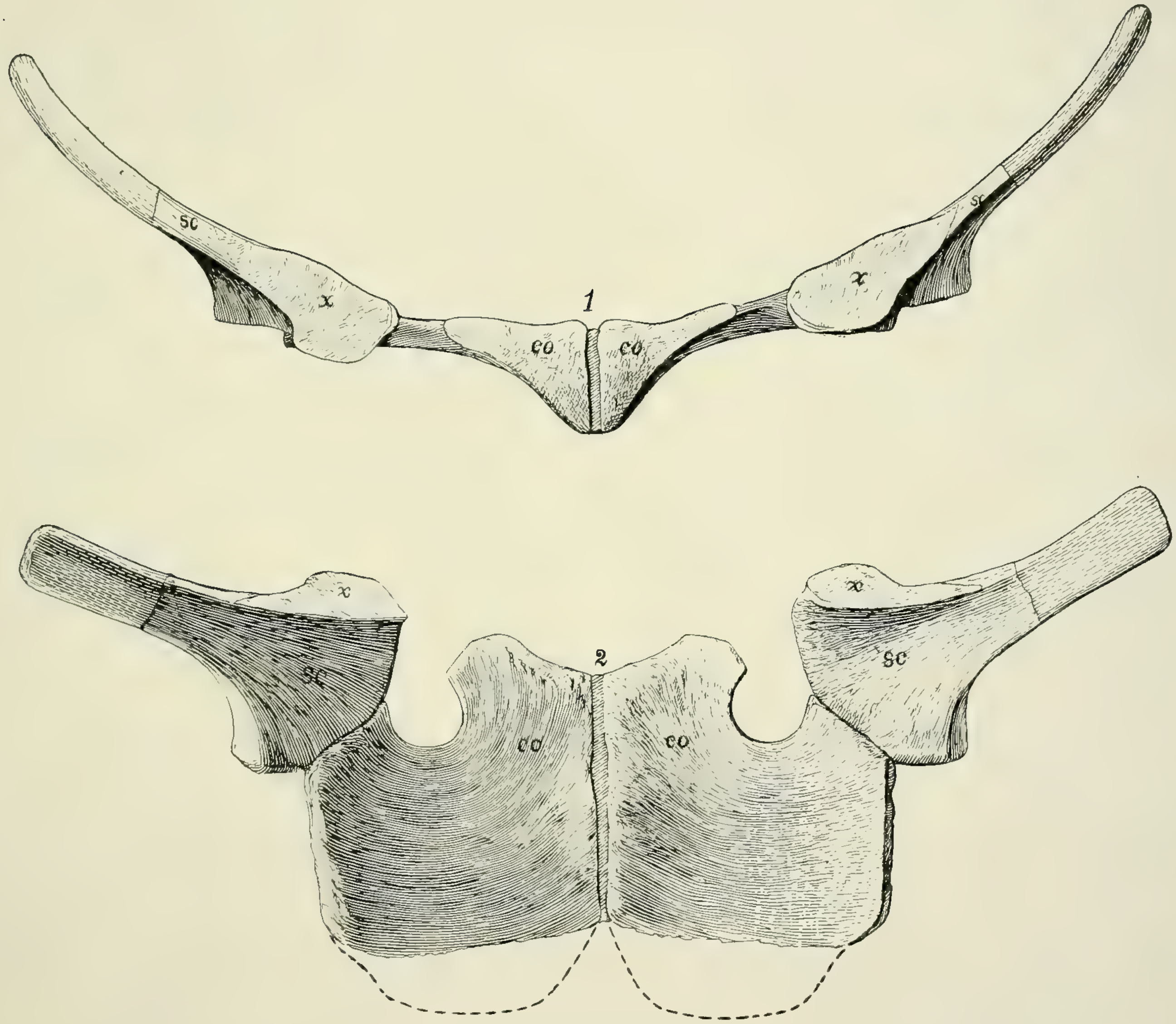


SKULL OF *BAPTANODON DISCUS*. 1, SUPERIOR VIEW (No. 878); 2, INFERIOR VIEW (No. 603). BOTH $\frac{1}{5}$ NATURAL SIZE. SOME SUTURES DRAWN AFTER No. 1441.

EXPLANATION OF PLATE XXXVIII.

1. Anterior view of pectoral girdle of *Baptanodon robustus* (No. 919). Type. One fifth natural size. *co.*, coracoids; *sc.*, scapulæ; *x.*, surfaces for attachment of the clavicles.

2. Dorsal view of the same girdle. One fifth natural size. *co.*, coracoids; *sc.*, scapulæ; *x.*, surfaces for attachment of the clavicles.



PECTORAL GIRDLE OF *BAPTANODON ROBUSTUS* (TYPE SPECIMEN). 1, ANTERIOR VIEW; 2, DORSAL VIEW (No. 919). BOTH $\frac{1}{5}$ NATURAL SIZE.

Publications of the Carnegie Museum. Serial No. 44.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 10.

W. J. HOLLAND, EDITOR.

THE CRAWFISHES OF THE STATE OF PENNSYLVANIA

BY A. E. ORTMANN, PH.D.

TITLE PAGE, TABLE OF CONTENTS, AND INDEX OF VOL. II.

PITTSBURGH.
PUBLISHED BY THE AUTHORITY OF THE BOARD OF TRUSTEES OF THE
CARNEGIE INSTITUTE.
DECEMBER, 1906.

FEB 28 1907
National Museum.

PRICE LIST OF PUBLICATIONS OF THE CARNEGIE MUSEUM

ANNUAL REPORTS OF THE DIRECTOR

1898, 30c. (scarce); 1899, 25c.; 1900, 30c. (scarce); 1901, 25c.; 1902, 25c.; 1903, 25c.; 1904, 25c.; 1905, 25c.

REPORTS OF THE PRIZE ESSAY CONTEST

1897 (out of print); 1898 (out of print); 1899, 30c. (scarce); 1900, 25c.; 1901, 25c., 1902, 25c.; 1903, 25c.; 1904, 20c.

REPORTS OF PROCEEDINGS OF FOUNDER'S DAY

1898, 35c.; 1899, 35c.; 1901, 35c.; 1901, 35c.; 1902, 35c.; 1903, 35c.; 1904, 35c.; 1905, 35c.

ANNALS OF THE CARNEGIE MUSEUM

The Annals are supplied to those who subscribe in advance in parts (paper-bound), as published, at $3.50 per volume.

VOL. I.

Part 1, unbound (scarce)	$1.50
" 2, "	1.00
" 3, "	1.00
" 4, "	1.00
Bound Green Cloth, 8vo, pp. 536, 25 Plates	4.00
" ½ Morocco do do	4.50

(The Edition in ½ Morocco is exhausted).

VOL. II.

Part 1, unbound	$1.00
" 2, "	1.00
" 3, "	1.00
" 4, "	1.00
Bound Green Cloth, 8vo, pp. 613, 20 Plates	4.00
" ½ Morocco do do	4.50

VOL. III.

Part 1, unbound	$1.00
" 2, "	1.00
" 3, "	1.00
" 4, "	1.00
Bound Green Cloth, 8vo, pp. 623, 25 Plates	4.00
" ½ Morocco do do	4.50

VOL. IV.

Part 1 (In Press)	$1.00

(Subscriptions for Volume IV, unbound, will be received at $3.50.)

MEMOIRS OF THE CARNEGIE MUSEUM

The Memoirs are supplied to those who subscribe in advance in parts (paper-bound), as published, at $10 per volume.

VOL. I.

No. 1. **Diplodocus, Its Osteology, Taxonomy, and Probable Habits, with a Restoration of the Skeleton.** By J. B. Hatcher. (*Very scarce*)	$3.00
No. 2. **Oligocene Canidæ.** By J. B. Hatcher	1.50
No. 3. **The Osteology of the Steganopodes.** By R. W. Shufeldt	2.75
No. 4. **Classification of the Chalcid Flies.** By W. H. Ashmead	6.50

Vol. I. Bound Green Cloth, large 4to, pp. 555, 39 Plates, can be supplied at $10.75 per volume; Bound ½ Morocco at $11.50.

MEMOIRS

OF THE

CARNEGIE MUSEUM.

VOL. II. NO. 10.

THE CRAWFISHES OF THE STATE OF PENNSYLVANIA.

By Arnold E. Ortmann, Ph.D.

I. Introduction.

The present Memoir is a continuation of, and an enlargement upon, the preliminary paper published some time ago in the Annals of the Carnegie Museum (Vol. III, 1905, p. 387 *et seq.*) under the title "The Crawfishes of Western Pennsylvania." The object of these publications is to furnish the student with an account of the crawfish-fauna of the state of Pennsylvania as complete as possible, not only from the morphological and zoögeographical, but also from the biological, ecological, and economic standpoint. It is now believed that it is possible to present an approximately complete report upon this important branch of the fresh-water fauna of the state, and in the prosecution of the studies of the author a number of questions were raised, the solution of which proved to be highly interesting.

It may be well at the beginning to give an outline of the work done. At the outset the writer resolved to go over the whole state, and to collect specimens in as many different localities as possible. Very soon, however, it was discovered that the different parts of the state are of unequal interest. Large tracts, located chiefly in the central, northern, and northeastern parts of the state, proved to be rather uninteresting, only one species of crawfish being present in them, while the western, and chiefly the southwestern, and again the southeastern sections offered more variety. Thus it became necessary to pay more attention to the latter areas. The uninteresting regions were entered only in a few cases, but a good deal of work was done around their edges, in order to trace their limits as accurately as possible.

The location of the writer in Pittsburgh was advantageous, being central within that section of the state which offered the greatest number of problems. Most of the collecting excursions were undertaken with Pittsburgh as a base. However, on three occasions the base was shifted. Visits were twice made to the eastern part of the state, where the writer spent several weeks in September of the years 1904 and 1905 in Philadelphia and its environs, and once to the eastern central part, where several days were spent in Harrisburg in June, 1905. The latter visit was marred by rainy weather.

The work of collecting was done for the Carnegie Museum by the writer in connection with his duties as Curator of Invertebrate Zoölogy, and all the necessary expenses were paid by the Museum. In order to give an idea of the amount of field-work done, a few statistics may be interesting.

Altogether one hundred and thirty-eight days were spent in the field, counting only those days on which actual collecting was done: four days in 1903; sixty in 1904; and seventy-four in 1905. A few additional records were obtained in 1906.

The distances covered in travelling were as follows:

		Total.
By rail, in 1904	3238 miles.	
" " " 1905	7579 "	10,817 miles.
By team, in 1904	12 miles.	
" " " 1905	26 "	38 miles.
On foot, in 1903	3 miles.	
" " " 1904	173 "	
" " " 1905	209 "	385 miles.
Grand Total		11,240 miles.

Collections were made at about one hundred and fifty-six different localities, most of them in the state of Pennsylvania. Of the sixty-seven counties of the state thirty-nine were visited.[1] Besides, visits were made to a number of localities situated in neighboring states, namely: in Camden County, New Jersey; in Allegheny and Garrett Counties, Maryland; in Morgan, Mineral, Tucker, Preston, Monongalia, Pleasants, Wetzel, Marshall, Ohio, Brooke, and Hancock Counties, West Virginia; and in Harrison, Carroll, and Stark Counties, Ohio.

The material secured on these excursions belongs to and has been deposited in the collections of the Carnegie Museum, and comprises 303 entries in the Catalog, including 1869 specimens. But this does not represent the entire number of specimens collected, since large sets, which have not been cataloged, have been set aside as material for exchange, study, etc.

---

[1] Material was secured, seen, or was previously known from fifteen additional counties, so that only thirteen are not explored, namely: Carbon, Juniata, Lackawanna, Lebanon, Mifflin, Monroe, Montour, Pike, Schuylkill, Snyder, Susquehanna, Union, and Wyoming. All these belong to the central and northeastern section of the state, where only one species of Cambarus (*C. bartoni*) is to be expected, with the exception of those localities which are in the immediate vicinity of the main branches of the Susquehanna River, where also *C. limosus* may be present (Juniata, Montour, Snyder, and Union Counties).

Practical experience gradually revealed to the writer the best method of collecting crawfishes. At first the writer was rather inexperienced, and did not know where to look for certain species. But the necessary knowledge and skill were soon acquired.

To collect the species living in streams, rivers, and ponds requires no special effort; it is only necessary to wade into the water-course to be investigated, or to walk along its edge, and to discover the hiding-places of the crawfishes, which is done by turning over stones. A pair of rubber-boots, or wading-stockings, protected by ordinary bathing-shoes, is very convenient; and also a small landing-net, the bag made of minnow-netting. Frequently specimens may be caught with the hand. In certain places, and in the case of certain species (*Cambarus limosus*) water-weeds often furnish hiding-places, and here it is advisable to use a larger landing-net with a long handle, which is pulled or pushed through the weeds.

More work is required in collecting the burrowing species. The first thing is to locate them, which is generally done by searching for the mud-chimneys built over their burrows. But it is not always easy to find these, particularly in late summer and autumn, the chimneys being then rather inconspicuous. I generally first ascertain favorable localities, such as swampy places in the bottom-lands, and springy places on the hillsides. It is a very good plan to closely watch ditches by the roadsides. Here the chimneys generally are easily detected, and in the neighborhood of such places large colonies often may be found. After a burrowing form has been located, the most difficult work begins, for the inhabitant of the burrow must be dug out of its hiding-place. Care must be taken while digging not to injure the crawfish. Sometimes the work can be done with the bare hand, but only in those rare instances in which the burrows are in very soft ground. Generally the work must be done with pick and shovel, but, as it is inconvenient to carry these cumbersome tools along on an excursion and a gardener's trowel is a little too weak, I have found a pioneer's bayonet, such as is used in the United States Army, to be a tool which beautifully serves the purpose. These bayonets may be had in gun- and ammunition-stores in the larger cities, and are practically indestructible.

After locating a crawfish-hole, I begin to dig down around it, loosening the dirt with the bayonet, and removing it with my hands, always taking care not to lose trace of the hole. Generally it is necessary to go down upon the knees (rubber boots are useful here), and even the belly, in order to reach the bottom of the hole, to which the crawfish usually retreats when disturbed. Often, however, it retires to a side branch, in which case it is not necessary to dig so deep. As soon as it is felt beginning to pinch with its claws, it is a sure sign that the crawfish has been cornered, and cannot retreat further. It is then readily secured, but care must be taken not to pull it out by the claws, which may be easily broken off, thus damaging the specimen. The creature should be always seized by the carapace.

Sometimes this work is very difficult and tedious, and I have often been compelled, chiefly in the case of *Cambarus carolinus*, to dig as deep as three feet before succeeding in capturing the crawfish. In order to avoid unnecessary labor as far as possible, I select burrows in which the water stands near the surface, refusing those which evidently go for a long distance through dry soil. Generally there is ample opportunity to choose between the numerous burrows of one and the same colony of chimney-builders. Now and then it happens that the work is rendered easier by the action of the crawfish itself. It occasionally comes to pass that, after having disturbed the entrance of the hole by digging down far enough to reach the water, the crawfish may be seen coming forward, apparently trying to ascertain the the cause of the disturbance. This is a good chance to seize it, but one must be quick, since it generally is the only chance to get it easily, although I remember cases when the crawfish came out again and again, just so far as to be plainly seen, but darted back at every attempt to seize it. Males are more frequently caught in this way than females, and such captures are made most frequently in cloudy or rainy weather. It is very rarely that there is a chance to capture the crawfish at the mouth of the undisturbed hole, when it is sitting at or near the top of the chimney, or on the ground away from the hole. This happened only once or twice in my experience.

I have tried to discover means of compelling the crawfish to come out of its burrow, but without much success. Bisulfide of carbon will not avail since it floats upon water. I tried chloroform, which sinks in water, but without success. Only once had I the satisfaction of driving a specimen of *Cambarus monongalensis* out of its hole by using unslacked lime. In this case I had dug a hole nearly three feet deep without being able to reach the bottom. I happened to have with me, especially for this purpose, a small tin box with unslacked lime, and dropped the contents into the hole, where it apparently sank to the bottom. Within three or four minutes the crawfish was discovered hurriedly working its way upward in the hole, and was easily taken. This method, however, can be used only in a limited way, since the holes generally are not straight enough to afford a chance to drop the lime to the bottom, and, if the lime becomes lodged somewhere above the point where the crawfish is staying, it drives it away from the mouth of the hole, and eventually kills it before it can be reached. (As to the use of lime for destroying crawfishes, see *infra*, VI, 4.)

The tools and the outfit needed for collecting crawfishes consist of rubber-boots (for work in swamps), or wading-stockings with low shoes (for work in streams), bayonet (for digging up burrowing species), and a landing-net with minnow-netting. These are indispensable. Further, a number of collecting jars are needed, with 75 per cent. to 80 per cent. alcohol, and I prefer to carry them in an ordinary fishing-basket, but any other portable receptacle will do. I do not recommend the use of formaldehyde, since it makes the specimens too brittle. In order to take specimens home alive, a so-called "bait-box" is most convenient.

I have no experience in baiting crawfish, and never attempted it, since the methods described above proved satisfactory. Furthermore, I have never (in Pennsylvania) used the seine, and I do not think that this would be necessary or advisable in this part of the country, although it may be tried to advantage elsewhere.

Besides the material secured by me in the manner above related, I made use of the older material preserved in the Carnegie Museum, which was collected by the following gentlemen: D. A. Atkinson, G. H. Clapp, E. Frost, B. Graf, J. L. Graf, E. Hays, S. N. Rhoads, A. T. Shafer, Q. T. Shafer, H. H. Smith, R. Taylor, W. E. C. Todd, M. A. Wertheimer, and E. B. Williamson.

I was aided in my researches by material kindly collected by various persons for the Museum, while my work was in progress, and to all of them I wish to here express my best thanks. They are the following members of the Museum staff: Mrs. Elizabeth Courtney, Mr. C. V. Hartman, Mr. D. C. Hughes, Mr. O. E. Jennings, and Mrs. O. E. Jennings.

The following gentlemen living in or near Pittsburgh furnished material: Dr. D. A. Atkinson, Dr. O. T. Cruikshank, Mr. R. Dornberger, Mr. D. Friel, Mr. F. E. Kelly, Dr. A. Koenig, Mr. A. Settlemoyer, and Mr. R. Settlemoyer.

Material from other parts of Pennsylvania was received from Professor A. E. Davison, Lafayette College, Easton, and Mr. H. Gera, Manayunk.

Specimens of our Pennsylvanian species were received from localities outside of the State from the following sources: Academy of Natural Sciences, Philadelphia, (material from Delaware, Maryland, and North Carolina, in exchange); Mr. H. Gera, Manayunk, (material from New Jersey); the late Mr. J. B. Hatcher, Pittsburgh, (material from Iowa); Mr. O. E. Jennings, Pittsburgh, (material from Ohio); Mr. S. Prentice, Pittsburgh (material from Kansas); Dr. R. Ruedemann, Albany, New York, (material from New York); Mr. F. Silvester, Princeton, New Jersey, (material from Maryland); Mr. E. B. Williamson, Bluffton, Indiana, (material from Kentucky, Indiana, and Michigan).

Very considerable help was received from the Department of Agriculture in Harrisburg. The State Zoölogist, Professor H. A. Surface, not only sent to me for inspection all the crawfishes in the collection under his charge, but also submitted to me material collected during the summer of 1905 by Mr. W. R. McConnell, who was in charge of a survey conducted by the State Zoölogist in coöperation with the Commissioner of Fisheries, Mr. W. E. Meehan. To Mr. Meehan and Professor Surface I am under special obligation for giving instructions to Mr. McConnell regarding the collecting of crawfishes, and to the latter gentleman for carrying these out in the most thorough way in parts of the state not visited by myself.

Finally, I was granted the privilege of examining the collections of the Academy of Natural Sciences in Philadelphia, where I found, aside from older specimens already used by Hagen and Faxon, valuable additional material, collected by Messrs. H. A. Pilsbry, E. G. Vanatta, H. W. Fowler, and B. W. Griffiths. I also received specimens for examination from Oberlin College, through the late Professor A. A. Wright and Mr. R. L. Baird; from the New York State Museum through Mr. F. C. Paulmier; and from Dr. P. R. Uhler in Baltimore, and Professor T. D. A. Cockerell, in Boulder, Colorado.

Last, but not least, my thanks are due to the Director of the Carnegie Museum, Dr. W. J. Holland, who not only granted the means for carrying on my work successfully, but has devoted much time to the editorial revision of the manuscript, and helped me in the preparation of the colored plates accompanying this memoir, which were made under his direction.

II. Historical Review of our Systematic Knowledge of the Crawfishes of Pennsylvania.

The first species of the genus *Cambarus* ever described very likely came from our state. *Astacus bartoni* of Fabricius (1798, p. 407) was sent to its author by Professor B. Smith Barton, who lived in Philadelphia, (see Faxon, 1885*a*, p. 65) and presumably was collected in the neighborhood of that city.

The next record of a Pennsylvanian crawfish is given by Rafinesque (Nov., 1817), *Astacus limosus*, from the muddy banks of the Delaware near Philadelphia. Another species mentioned by Rafinesque from this state, *Astacus fossor*, is not recognizable. *Astacus limosus* from the Delaware River was described a month later (Dec., 1817) by Say under the name of *Astacus affinis*.

Harlan (1835) mentions *A. bartoni* from the vicinity of Philadelphia, and this record makes Philadelphia the type-locality of this species.

Girard (1852) gives the following new localities in Pennsylvania: *Cambarus* *affinis* = *limosus*, Schuylkill River at Reading, Bucks County; *C. bartoni*, Foxburg, Clarion County; Carlisle, Cumberland County; Berwick, Columbia County.

In Hagen's Monograph (1870) no new species are added, although he doubtfully records (p. 100) *C. obscurus* from the state, but this was done under the erroneous assumption that *Astacus fossor* of Rafinesque is the same as *C. obscurus*. Thus Hagen's Monograph adds only a few new localities, namely: for *C. limosus* (*affinis*) the Schuylkill River, Philadelphia, and Carlisle, Cumberland County. The new locality "Pittsburgh" for the same species is wrong.

The great revision of the genus published by Faxon (1885*a*) adds two species: *C. diogenes* from Derry, Westmoreland County, and *C. rusticus* from Pittsburg. The latter record is incorrect, and should be dropped. Besides Faxon gives the following new localities: *C. limosus*, Brandywine Creek, Chester County; Delaware River, Bristol, Bucks County; Bainbridge, Lancaster County; *C. bartoni*, Bedford and Pattonville, (see *infra*, foot-note 16), Bedford County; Windham, Bradford County; Hummelstown, Dauphin County; Chester County; Bainbridge, Lancaster County; McKean County.

Thus only three species were known up to this date: *C. limosus*, *C. bartoni*, and *C. diogenes*.

In 1898 Faxon added a fourth species for the state, *C. obscurus* from Westmoreland County, and also gave a new locality for *C. bartoni*, Westmoreland County.

Williamson (1901) enumerated five species, and one variety from Allegheny County, but, as has been demonstrated by the writer (1905*a*), this is to be reduced to four species and one variety, of which the species recorded as *C. dubius* by Williamson (*C. monongalensis* Ortmann) is new for the state, as is also the variety *C. bartoni robustus*. Allegheny County is for the first time cited as a locality for the other species, *C. obscurus* (recorded as *C. propinquus* and *rusticus*), *C. bartoni*, and *C. diogenes*. Williamson's discoveries brought up the number of species known from the state to five, and one variety, namely: *C. limosus*, *C. obscurus*, *C. bartoni*, *C. bartoni robustus*, *C. monongalensis* (as *dubius*), and *C. diogenes*.

In the preliminary report of the writer for western Pennsylvania, two other species were added: C. *propinquus* from Erie and Crawford Counties, and *C. carolinus* from Fayette, Westmoreland, and Somerset Counties. Numerous new localities were added to those already known. *C. dubius* of Williamson was recognized as a species new to science, and described as *C. monongalensis*. The number of species present in the state has not been increased by subsequent investigations, and stands now as seven, with one variety, namely: *Cambarus limosus* (Rafinesque); *C. propinquus* Girard; *C. obscurus* Hagen; *C. bartoni* (Fabricius); *C. bartoni robustus* (Girard); *C. carolinus* Erichson; *C. monongalensis* Ortmann; *C. diogenes* Girard.

These eight different forms are treated in the following pages, with the addition of one extralimital form, a variety of *C. propinquus* (*C. propinquus sanborni*). The recent and past observations made by the writer, together with those collated from other sources, are presented as completely as possible in the succeeding pages, thus giving a natural history of this group of animals, so far as found in the state of Pennsylvania. It has always been the aim of the writer to support his conclusions by evidence secured within the state, but observations made outside of the state are sometimes introduced, where a gap was to be filled, or where they were of special interest.

III. Morphology and Chorology of the Pennsylvanian Species.

A. *General Remarks.*

The crawfishes (as to the use of "crawfish" in preference to "crayfish" see *infra*, VI) of the state of Pennsylvania belong to the genus *Cambarus*[2] of Erichson (1846), of the family *Potamobiidæ* Huxley, including the freshwater crawfishes of the northern hemisphere. Faxon (1898) regards this as a subfamily, *Astacinæ*, of the family *Astacidæ*, which also includes the subfamily, *Parastacinæ* of the southern hemisphere, now regarded as a family, *Parastacidæ* Huxley. There is some discussion as to the proper name of the family, depending on the use of the generic name *Astacus* Fabricius, or of *Potamobius* Samouelle, for the European crawfishes. The position of the writer was defined in 1902, (*Proc. Amer. Philos. Soc.* XLI, p. 276, footnote). The question, however, has recently been finally settled by a discovery made by Miss M. J. Rathbun (*Proc. Biol. Soc. Washington*, XVII, 1904, p. 170), but not in the manner suggested by Miss Rathbun. The fact that the name *Homarus* was used first by Weber (*Nomenclator Entomologicus*, 1795), in place of *Astacus* Fabricius, 1775, makes *Homarus* a pure and simple synonym of *Astacus*, and according to the rule "once a synonym, always a synonym," it remains a synonym. There is no reason to make it "desirable," as Miss Rathbun expresses it, to set aside the rule in this case,

The genus *Cambarus*, containing now about 70 species, has been variously subdivided: by Girard (1852) into three groups; by Hagen (1870) likewise into three groups, which, however, do not exactly correspond to those of Girard; and by Faxon (1885*a*) into five groups. Recently the present writer has divided the genus into six subgenera, namely: *Paracambarus*, *Procambarus*, *Cambarus*, *Cambarellus*, *Faxonius*, *Bartonius*. (See *Proc. Am. Phil. Soc.*, XLIV, 1905, p. 91, *et seq.*; *Ann. Carn. Mus.* III, 1905, p. 437; and *Proc. Washington Acad. Science*, VIII, p. 1, 1906.)

---

[2] Erichson made this provisionally a subgenus, but expressed the opinion that it perhaps would better rank as a genus. Girard (1852) was the first to use *Cambarus* as a generic name.

Only the two last named subgenera, *Faxonius* and *Bartonius*, are found within the boundaries of the state of Pennsylvania, and they are distinguished from the rest by the shape of the male copulatory organs. The latter consist of two parts, which are completely separated at the tips for a shorter or longer distance, and never possess any accessory spines. The outer part in the male of the first form, (sexually ripe), is almost completely transformed into a horny spine, while the inner remains soft. In the Pennsylvanian species of these two subgenera only the third pereiopods possess a hook (used to take hold of the female) on the ischiopodite.

The two subgenera are distinguished as follows:

Subgenus *Faxonius* Ortmann.

Sexual organs of first pair in the male with two shorter or longer completely separated tips. Tips straight or gently curved, divergent, parallel, or convergent, generally rather slender.

Subgenus *Bartonius* Ortmann.

Sexual organs of the first pair in the male with two rather short, completely separated tips. Both tips are strongly recurved, forming with the basal part about a right angle.

B. *Key to the Pennsylvanian Species of the Genus Cambarus.*

a′. Sexual organs of male of the *Faxonius*-type. Rostrum always with a marginal spine on each side, and carapace with one or more lateral spines. (River species.)

b′. Tips of sexual organs short, straight, and divergent. Sides of carapace with several lateral spines anterior to, and behind the cervical groove. (Delaware, Susquehanna, and Potomac drainages.)
C. (*Faxonius*) *limosus* (Rafinesque).

b′′. Tips of sexual organs long, almost straight, slightly convergent, or parallel. Sides of carapace with only one spine behind the cervical groove.

c′. Rostrum with median keel. Sexual organs of male of first form at anterior margin without prominent angle (shoulder). Annulus ventralis of female flat. (Lake Erie and its drainage.)
C. (*Faxonius*) *propinquus* Girard.

c′′. Rostrum without median keel. Sexual organs of male of first form at anterior margin with a prominent angle (shoulder). Annulus ventralis of female with two tubercles in anterior part. (Ohio drainage).
C. (*Faxonius*) *obscurus* Hagen.

a′′. Sexual organs of male of the *Bartonius*-type. Rostrum always without marginal spines. Carapace generally without lateral spines.

b′. Areola wide. Form of carapace depressed. Color brownish or greenish. (Species of the small streams.)
C. (*Bartonius*) *bartoni* (Fabricius).

b′′. Areola narrow or obliterated in the middle. Form of carapace rather compressed. (Burrowing species.)

c′. Areola narrow. Inner margin of hand generally with only one row of tubercles. Color very bright, of tints unusual among crawfishes.

d′. Color red. Rostrum short and very broad. Outer margin of hand serrated. (Mountains of southern Pennsylvania). C. (*Bartonius*) *carolinus* Erichson.

d′′. Color blue. Rostrum short and narrower. Outer margin of hand rounded, not serrated. (Hills of southwestern Pennsylvania.) C. (*Bartonius*) *monongalensis* Ortmann.

c''. Areola generally obliterated in the middle, or extremely narrow. Inner margin of hand with several rows of tubercles. Color greenish or brownish. Rostrum rather long and narrow. (Swamps on hills and in lowlands, southwestern and eastern Pennsylvania.) *C.* (*Bartonius*) *diogenes* Girard.

C. Description and Distribution of the Species.

1. CAMBARUS (FAXONIUS) LIMOSUS (Rafinesque).

(Plate B, Fig. 3; Plate XXXIX, Figs. 5*a* and 5*b*.)

Astacus limosus Rafinesque, 1817, p. 4[illegible].

Astacus affinis Say, 1817, p. 168; Harlan, 1835, p. 230, fig. 2; DeKay, 1844, p. 23; Gibbes, 1850, p. 195 (*partim*).

Astacus bartoni Milne-Edwards, 1837, p. 331 (*non* Fabricius).

Cambarus affinis Girard, 1852, p. 37; Hagen, 1870, p. 60; Pl. 1, figs. 19, 22, 84, 85, Pl. 3, fig. 152, Pl. 5; Abbott, 1873, p. 80; Smith, 1874, p. 638; Faxon, 1884*b*, p. 146; Faxon, 1885*a*, p. 86; Faxon, 1885*b*, p. 360; Underwood, 1886, p. 366; Faxon, 1890, p. 628; Hay, 1899, p. 960, 964; Andrews, 1894, p. 165.

Cambarus pealei Girard, 1852, p. 87.

Cambarus (*Faxonius*) *limosus* Ortmann, 1905*b*, p. 107, 112, 131.

Body robust, pubescent all over, but chiefly so on carapace and chelæ; but the pubescence wears off easily, and in old individuals, especially in early spring, the body is more or less hairless. The hairs are most persistent on the fingers of the large chelæ.

Carapace subovate, depressed, the depression being brought about by a bulging out of the branchial regions. The vertical height of the carapace, at a point about in the middle of the gastric region (measured from this point to a point on the sternum just in front of the first pereiopods), the vertical height of the carapace at a point of the areola directly above the sternum between the second pereiopods, and the greatest width of the carapace at the hepatic regions are about the same; while the greatest width of the carapace at the branchial regions is distinctly greater. Relation $G:H:B = 1:1:1.2$ to 1.4.[3] The greatest width of carapace (at branchial regions) is well behind, at about the middle of the branchial regions. The whole carapace appears rather flattened dorsally.

Cervical groove deep, continuous on the sides. *Areola* about half as long as anterior section of carapace (including rostrum). Relation of $a:p = 1:0.40$ to 0.55.[4] Areola rather broad, relation of $w:l = 1:4.0$ to 5.4,[5] with about 5 irregular rows of punctures.

Rostrum long and broad, reaching to the middle of the fifth joint of the peduncle of the antenna, and to the end of the peduncle of the antennula, rarely slightly

[3] G = vertical diameter at gastric region; H = transverse diameter at hepatic region; B = transverse diameter at branchial region.

[4] a = anterior, p = posterior section of carapace.

[5] w = width, l = length of areola.

longer. Surface deeply concave, margins elevated and thickened, almost straight, very little convergent toward the marginal spines. Marginal spines well developed. Acumen long, triangular, acutely pointed, about one third as long as the whole rostrum, sometimes slightly shorter or longer. *Post-orbital ridges* parallel, ending in a sharp spine anteriorly.

Surface of carapace finely punctate, and very finely granulate on the sides in old specimens. Sides spinose. There are a number of larger and smaller spines on each side on the hepatic region, and a few spines are found on the branchial region immediately behind the cervical groove, of which one is generally much larger than the others. (In most cases there are two distinct spines, one above the other, the lower one the larger.) All these spines are well developed only in larger individuals; in young ones only two spines behind the cervical groove and one spine on the hepatic region are present, but these are visible even in the smallest specimens at hand (25 mm. long). External orbital angle not marked, rounded off. Branchiostegal spine sharp and distinct.

Abdomen longer than the carapace, slightly narrower than the carapace in the male, slightly wider in the female. Anterior section of telson on the outer posterior corners generally with two spines, but there may be from one to three; the number of spines may differ on either side. Posterior section of telson semicircular, slightly wider than long, and slightly shorter than anterior section.

Epistoma with posterior part short and broad, almost three times as wide as long, not plane, with a transverse groove posterior to the middle, and an anterior median depression; these are often united into a triangular or arrow-shaped depression. Anterior section constricted at base, its anterior margin almost semicircular, with a small median point, slightly varying in shape (sometimes it is subtriangular, sometimes the anterior point is obscure), but its transverse diameter is always slightly greater than the longitudinal.

Antennula with a sharp spine on the lower margin of the basal joint.

Antennal peduncle with a sharp spine on the outer side of each of the two basal joints.

Antennal scale long, as long as the rostrum or even slightly longer, reaching to the middle or the end of the terminal joint of the antennal peduncle. Outer margin with a strong spine. Laminar part rather broad; its margin more or less regularly curved; the broadest part is in the middle or slightly anterior to it.

Flagellum, when laid backward, reaching to the fourth or even to the middle of the fifth abdominal segment in the male; in the female it generally does not reach beyond the posterior margin of the third segment.

First pereiopods comparatively short, and not very stout, considering the size of the species. Hand short and not very broad, depressed, elongate-ovate, stronger and more elongate in the male than in the female. Surface punctate. Inner margin almost straight, with a double row of tubercles, which are more or less spiniform. Outer margin smooth, bluntly angular, more distinctly so distally. Fingers distinctly longer than the palm (measured from articular tubercle on upper side of carpopodite to articular tubercle on upper side of palm at base of movable finger), straight, cutting edges straight, in contact all along their length, with a few very small tubercles in the proximal part, for the rest without teeth or tubercles, but with a short and dense pubescence, becoming slightly barbate proximally on lower side. Upper surface of each finger with a low longitudinal rib, most distinct distally. Lower surface of hand almost smooth, sparsely punctate.

Carpopodite slightly longer than wide, shorter than palm, punctate. Upper surface with a distinct longitudinal sulcus. Inner margin with a strong procurved spine in the middle, and a small spine anterior to it. Lower surface with two strong spines, one in the middle of the anterior margin, the other at articulation with hand. Sometimes there are additional small spines or spiniform tubercles, proximal to, or above, the large spine of the inner margin.

Meropodite smooth, upper margin with two (rarely more, up to four) strong spines at a short distance from the distal end. Lower margin with two rows of strong spines, the inner one consisting of four to ten spines, largest distally, the outer one of two to three spines. A spine at the outer articulation with the carpopodite.

Ischiopodite of third pereiopods hooked in the male; hook in the male of the first form strong, subconical.

Coxopodites of posterior pereiopods without prominent crests or tubercles in the male.

First pleopods of male of the first form (Plate I, Fig. 5*a* and 5*b*) rather strong and short, not reaching beyond the anterior margin of the coxopodites of the third pereiopods. They are not articulated at the base, straight, and the two parts are separated at the tips only for a short distance. Tips crossed (twisted), divergent; that of the inner part is soft, gradually tapering to a point, and is directed obliquely outward; that of the outer part is horny, gradually tapering to a point, and directed obliquely forward and slightly inward.

In the male of the second form the first pleopods are articulated at the base when young, but not articulated when old, and both tips are soft; that of the outer part is rather bluntly pointed.

Annulus ventralis of female transversely rhombiform, with a short transverse groove slightly posterior to the middle, and an S-shaped longitudinal fissure. Anterior to the central groove there is on each side of the fissure a strong, tuberculiform elevation, so that the fissure is situated in a rather deep depression. Posterior to the central groove, there is a slight elevation, over which the fissure passes. The annulus, consequently, appears trituberculate, the two anterior tubercles being stronger than the posterior. In young females, the tubercles are only slightly developed, and generally the posterior tubercle is almost obsolete.

Size. — Rafinesque gives as total length 3–9 inches. The maximum, 9 in., = 229 mm., seems rather strange, since no such specimens have ever been subsequently seen, even if we infer that Rafinesque intended the whole length, including the claws. Hagen (1870, pl. 5) figures a very large female, which, including the outstretched claws, would not be longer than about 7 inches (178 mm.). Its body from the tip of the rostrum to the end of the telson, is 132 mm. long. The maximum length given by Hagen in the text (p. 61) is 4.7 in., = 119 mm; thus this figure, although said to be of natural size, is apparently somewhat enlarged.

The largest specimens ever seen by the writer are in the museum of Oberlin College from the Potomac River, a female measuring 120 mm., and a male of the first form measuring 105 mm. The largest specimen from Pennsylvania I possess, is a female from the Delaware River at Torresdale, and measures 93 mm. in length; the largest male (first form) is from the Delaware at Penns Manor, measuring 75 mm. in length. A male of the second form from Holmesburg is 85 mm. long. Specimens over 100 mm. long, mentioned by the writer, (1899, p. 1210), as from Philadelphia, are from the New Jersey side of the river, near Camden.

Colors. — (Plate B, Fig. 3.) An account of the color of this species has been given by Faxon (1885*a*, p. 88). It runs thus: "Upper surface greenish, mottled with darker green, especially on the chelæ; tips of fingers orange, preceded by a dark green ring, which runs along the outer border of the hand to the wrists; abdominal somites ornamented with interrupted transverse chestnut-colored double bands. Under surface of a lighter hue."

I have repeatedly made notes from live specimens, and have found that the shades of color vary greatly, although the general pattern has been correctly described by Faxon. The general color of the body may be described as *olive-green* (Ridgway, 1886, X, 18)[6], but it varies toward *tawny-olive* (III, 17), and *olive-yellow* (VI, 16). The sides of the carapace are generally lighter, of a whitish green.

---

[6] In the description of colors, I have used here (and in the following species) the nomenclature of Ridgway (1886), and the Roman and Arabic numerals refer to his plates and figures.

There is a brown (*chestnut*, IV, 9) spot on the anterior margin of the carapace on each side below the eyes, not noticed by Faxon. The brown bands of the abdomen are *burnt sienna* (IV, 6). In the middle of the abdomen the epimera are *hazel* (IV, 12). The color of the finger tips is *ferrugineous* (IV, 10), often paler, the preceding band is *dark olive-green*, often almost black. The articular tubercles on the lower side of the hand are *tawny* (V, 1), on the upper side they are *dark-green*. The articular membranes of the chelæ are *wine-purple* (VIII, 15). The darker green of the carapace is generally confined to distinct large blotches, symmetrically disposed; one pair on the gastric region, and one each on the anterior and the posterior part of the branchial regions. Often the two blotches of the gastric region run together, which may also be the case with those of the branchial regions. They often appear spotted or mottled with the lighter, or rather more brownish (tawny olive), ground color. The brown spot on the anterior margin of the carapace is sometimes indistinct, and in young specimens with fresh shells, it may have a trace of yellow below. All these colors are bright and distinct only in fresh shells. On old shells, a coat of mud is generally deposited, giving to the whole body a dirty blackish color, and besides, the colors themselves fade considerably, so that only a dirty olive-green remains, with some brown on the abdomen.

The color of newly laid eggs under the abdomen of the female is *olive-green* (X, 18).

The above description is founded upon the examination of one hundred and twenty-one specimens, now preserved in the collections of the Carnegie Museum. Fifty-six of these specimens are from the state of Pennsylvania, fifty-four from New Jersey, eight from Maryland, and three from West Virginia (Potomac River at Cherry Run, Morgan County). This, however, does not represent the total number of specimens seen by the writer, since many others were collected by him, as well as seen in the collections of the Department of Agriculture of Pennsylvania, of the Academy of Natural Sciences in Philadelphia, and of Oberlin College.

DISTRIBUTION.[7]

LOCALITIES REPRESENTED IN THE COLLECTIONS OF THE CARNEGIE MUSEUM.

PENNSYLVANIA: *Bucks Co.*, Delaware River, New Hope; Delaware River, Penns Manor; Little Neshaminy Creek, Grenoble; Common Creek, Tullytown; *Philadelphia Co.*, Delaware River, Torresdale Fish Hatchery, Torresdale; Delaware

---

[7] All localities without further record have been ascertained by the writer in person. In other cases the authority (when published), or the collector and institution, where the specimens are preserved, is given.

River, Holmesburg, (H. W. Fowler coll., exch. Acad. Phil. Nat. Sci.); Schuylkill Canal, Manayunk; *Montgomery Co.*, Schuylkill River, West Manayunk, (H. Gera coll.); *Delaware Co.*, Marcus Hook Creek, Marcus Hook; *Franklin Co.*, Back Creek, Williamson; *Bedford Co.*, Raystown Branch of Juniata River, Bedford (A. Kœnig coll.).

NEW JERSEY: *Camden Co.*, Delaware River, Camden; Delaware River, North Cramer Hill; *Mercer Co.*, Stony Brook, Princeton; Delaware-Raritan Canal, Aqueduct near Princeton.

MARYLAND: *Alleghany Co.*, Potomac River, Wiley's Ford, South Cumberland.

WEST VIRGINIA: *Morgan Co.*, Potomac River, Cherry Run.

PREVIOUS RECORDS.[8]

Type locality: Delaware River, Philadelphia, (Rafinesque).

PENNSYLVANIA: Schuylkill River, Philadelphia, (Hagen); *Bucks Co.*, Bristol, (Faxon); *Berks Co.*, Schuylkill River, Reading, (Girard); *Chester Co.*, Brandywine Creek, (Faxon); Tributary of Brandywine Creek, Chadds Ford Junction, (Ortmann); *Lancaster Co.*, Bainbridge, (Faxon); *Cumberland Co.*, Carlisle, (Hagen); *Adams Co.*, Gettysburg, (Ortmann).

NEW JERSEY: *Camden Co.*, Camden, (Faxon); *Burlington Co.*, Burlington, (Faxon); *Mercer Co.*, Trenton, (Abbott); *Monmouth Co.*, Red Bank, (Faxon); *Morris Co.*, Schooley's Mountain, (Faxon).

MARYLAND: *Cecil Co.*, (Faxon); *Hartford Co.*, Havre de Grace, (Hagen); *Baltimore Co.*, Baltimore, (Andrews); Guynn's Falls, (Faxon); Druid Hill, (Faxon); *Anne Arundel Co.*, (Faxon); *Charles Co.*, (Faxon); *Montgomery Co.*, (Faxon); *Washington Co.*, Williamsport, (Faxon); *Alleghany Co.*, Canal four miles south of Cumberland, (Faxon).

DISTRICT OF COLUMBIA: Washington, (Girard).

VIRGINIA: *Fairfax Co.*, Gunston, (Faxon); *Augusta Co.*, Shenandoah River, Waynesboro, (Faxon); *Isle of Wight Co.*, Blackwater River, Zuni, (Faxon).

NEW LOCALITIES NOT REPRESENTED IN CARNEGIE MUSEUM.

PENNSYLVANIA: *Montgomery Co.*, Roberts Run, Abrams, (B. W. Griffiths & H. W. Fowler, coll., Acad. Nat. Sci., Philadelphia).

The following records are from the collections of Mr. W. R. McConnell, belonging to the Department of Agriculture, Harrisburg: Yellow Breeches Creek, New Cumberland, Cumberland Co.; Conedogwinet Creek, West Fairview, Cumberland Co.; Sherman's Creek, Landisburg, Perry Co.; Montour Run, Greenpark, Perry

---

[8] A number of doubtful records have been dropped (see Ortmann, 1905*b*, p. 131). Too general records are also omitted, for instance: "Susquehanna River, Pa., (Faxon)," since just in this case more exact information is desired.

Co.; Susquehanna River, Northumberland, Northumberland Co.; Fishing Creek, Bloomsburg, Columbia Co.; Bald Eagle Creek, Milesburg, Center Co.; Conococheague Creek, Chambersburg, Marion, and Williamson, Franklin Co.; Maiden Creek, Maiden Creek, Berks Co.

REMARKS.

Cambarus limosus is the common river species of eastern Pennsylvania. Its morphological characters are very constant, and give it a rather isolated position within the genus, which is also expressed by, and very likely due to, its geographical isolation, the most closely allied species being found far to the west, in Indiana and Kentucky, (see Ortmann, 1905*b*, p. 114, 127). The most prominent specific characters are furnished by the male sexual organs, and the spinosity of the sides of the carapace. The description, as given above, does not indicate any important variations, and the specimens are generally very uniform. The spinosity of the carapace, however, changes with age, young specimens being much less spinose than old ones. In the spines of the chelipeds and of the anterior section of the telson, there is some variation, but this is only slight and not subject to any rule. The shape of the carapace and rostrum is very constant, the only differences of age noticed are found in the acumen of the rostrum, which in young specimens is slenderer than in those which are older, and in the bulging out of the branchial regions of the carapace, which is most marked in old individuals. The changes in the pubescence of the whole body are apparently due to wear. The short hairs generally present in newly moulted individuals slowly wear off, and specimens with a distinct coat of dirt upon them, indicating age, generally have the pubescence more or less, sometimes entirely, worn off. Only on the hands and fingers are traces of it left.

I myself have never found any freaks in this species. But Mr. W. R. McConnell found a male (first form), 66 mm. long, at Bloomsburg, Columbia County, (the only specimen taken at this locality), in which the rostrum had two pairs of marginal spines. The additional pair in this specimen is smaller, and stands about midway between the normal pair and the base of the rostrum.

2. CAMBARUS (FAXONIUS) PROPINQUUS Girard.

(Plate XXXIX, Fig. 6*a* and 6*b*.)

Cambarus propinquus, Girard, 1852, p. 88; Hagen, 1870, p. 67, Pl. 1, f. 34–38, Pl. 3, f. 153; Smith, 1874, p. 638; Forbes, 1876, p. 4, 19; Bundy, 1877, p. 171; Bundy, 1882, p. 181; Bundy, 1883, p. 402; Faxon, 1884, p. 147; Faxon, 1885*a*, p. 91; Faxon, 1885*b*, p. 360; Underwood, 1886, p. 371; Faxon, 1890, p. 628; Hay, 1896, p. 497, Fig. 11; Ward, 1896, p. 15; Faxon, 1898, p. 651; Hay, 1899, p. 960, 962; Ortmann, 1905*a*, p. 400.

Cambarus (*Faxonius*) *propinquus* Ortmann, 1505*b*, p. 112, 132.

Body not very robust, not pubescent, with only a few, scattered, short hairs, chiefly on the chelæ, but the hair wears off very soon, and the body becomes smooth, with exception of a slight pubescence at the base of the cutting edges of the fingers.

Carapace subovate, depressed. Relation $G:H:B = 1:1:1.2$ or 1.3. (The width of the branchial regions appears slightly less than in *C. limosus*, but this is probably due to the fact that the specimens of *C. propinquus* at hand are rather small). Greatest width of branchial regions well behind, at about the middle of the branchial regions. Carapace flattened dorsally.

Cervical groove deep, more or less distinctly interrupted on the sides just above the lateral spine. Posterior section of carapace about half as long as anterior (relation $a:p = 1:0.42$ to 0.62.

Areola rather broad, $w:l = 1:4.7$ to 6.0, with about four irregular rows of punctures.

Rostrum long and broad, reaching to the middle of the fifth joint of the peduncle of the antenna, and to the end of the peduncle of the antennula, sometimes slightly shorter. Surface concave, with a more or less distinct, low, longitudinal median keel toward the tip. Margins elevated, but not much thickened, straight, more or less convergent toward the marginal spines. Marginal spines generally well developed in young specimens, less so in older ones, sometimes quite small. Acumen long, triangular, comparatively longer in young specimens, pointed, about one-third as long as the whole rostrum, or shorter. Postorbital ridges slightly divergent posteriorly, ending anteriorly in a more or less distinct small spine.

Surface of carapace finely punctate, and slightly granulate on the hepatic regions in old specimens. Sides with only one spine on the branchial regions, immediately behind the cervical groove. This spine is always present and sharp, but generally not very large. No other spines on the sides of the carapace. External orbital angle not marked. Branchiostegal spine small, but sharp, or tuberculiform, or even obsolete.

Abdomen longer than carapace, slightly narrower than the carapace in the male, about as wide as the latter in the female. Anterior section of telson on the outer posterior corners with one to three spines (two spines is the general condition). Posterior section of telson semielliptical, considerably wider than long, and slightly shorter than anterior section.

Epistoma with posterior part short and broad, almost three times as wide as long, not plane, with a transverse groove and an anterior median depression running into each other. Anterior section constricted at base, its anterior margin generally almost semicircular, with a median point and an indistinct angle on each side, but shape rather variable: sometimes it is truncate anteriorly, with or without median point, the lateral angles being more distinct. Its transverse diameter is slightly greater than the longitudinal.

Antennula with a distinct, sharp spine on the lower margin of the basal joint.

Antennal peduncle with a distinct spine on the outer side of the first joint, and a smaller, sometimes tuberculiform spine on the second joint. *Antennal scale* long, as long as rostrum or slightly longer, reaching to the middle, or almost to the end of the terminal joint of the antennal peduncle. Outer margin with a strong spine. Laminar part rather broad, almost semicircular, the broadest part is slightly anterior to the middle.

Flagellum reaching to the beginning of the fifth abdominal segment in both the male and the female.

First pereiopods not very robust, comparatively longer in the male, shorter in the female. Hand elongate-ovate, depressed, moderately wide. Surface punctate. Inner margin almost straight, with a double row of tubercles. Outer margin smooth, marginated and bluntly angular, but almost evenly rounded near the proximal end. Fingers longer than palm, almost straight in the female, and meeting all along their edges; in the male, the fingers are slightly gaping at the base, and the movable one is slightly curved in the shape of an "S," which curve is chiefly noticeable along the outer margin. Outer margin of movable finger slightly tuberculate at base. Cutting edges with a few small tubercles near the base, for the rest slightly pubescent. Upper surface of each finger with a low, longitudinal rib. Lower surface of hand sparsely punctate.

Carpopodite slightly longer than wide, shorter than palm, punctate, and with a longitudinal sulcus on upper side. Inner margin with a strong, slightly procurved spine in the middle; generally there is a tubercle (rarely spiniform) anterior to this spine. Lower surface with a low and broad tubercle in the middle of the anterior margin, which is very rarely subspiniform; a similar tubercle with a spiniform tip at the articulation with the hand. No other spines or tubercles on the carpododite, except that sometimes there is a small tubercle at the proximal end of the inner margin.

Meropodite smooth; upper margin with two small, often indistinct, or tuberculiform, spines near the distal end. Lower margin with two rows of spines; the outer row consisting of only one, rarely of two, spines; the inner row consisting of a large distal spine, and a number (up to seven or eight) of very small ones, which may be entirely absent. Thus there are often only two anterior spines present, representing the distal spine of each row. A small spine at the outer articular tubercle with carpopodite.

Ischiopodite of third pereiopod hooked in the male, the hook in the male of the first form being strong, subconical.

Coxopodites of posterior pereiopods without prominent crests or tubercles in the male.

First pleopods of male of the first form (Plate XXXIX, Fig. 6*a*) slender, but rather short, hardly reaching beyond the middle of the coxopodites of the third pereiopods. They are not articulated at the base, and the two parts are completely separated at the tips for a rather considerable distance (about one third of the length from the inner basal tubercle to the tip). Both parts are almost parallel, only slightly convergent at the tips, which is due to a very slight curve of the outer part. Outer part gradually tapering from base to tip, horny. Inner part soft, of about the same shape as the outer, and of the same length, gradually tapering to an acute tip. Both parts are slightly twisted, so that the tip of the outer is directly anterior to that of the inner. Anterior margin of this organ without shoulder shortly below the point of separation of the two parts; sometimes, indeed, there is a slight notch, but never a sharp shoulder.

In the male of the second form, the first pleopods (Plate XXXIX, Fig. 6*b*) are articulated at the base when young, (only young specimens are at hand); both parts are separated only for a short distance, and are soft; the outer one is rather blunt, while the inner one tapers to a point. No notch or shoulder on anterior margin.

Annulus ventralis of female transversely rhombiform or ovate, rather flat, very slightly depressed in the middle, with an S-shaped longitudinal fissure. No tubercles on anterior part. In young females, the median depression is very indistinct, and the annulus is almost completely flat.

Size. — Hagen gives 2.6 in. = 66 mm. as the maximum length for this species. The largest individuals from the state of Pennsylvania observed by the writer, are a male (first form) from Albion, Erie County, 61.5 mm. long, and a female from the same locality 69 mm. long. I have seen, however, two larger males (first form) from Lake Erie, off the shore of Lorain County, Ohio (Mus. Oberlin), one measuring 77 mm., the other 81 mm. in length. Nevertheless, this seems to be one of the smaller species, for in the streams running to Lake Erie in Pennsylvania a considerable number of individuals have been taken, none of which was longer than the above mentioned specimens.

Colors. — The colors of this species agree closely with those of *C. obscurus* (which see for further particulars). The following notes were taken from an adult female, collected on the shore of Lake Erie at Miles Grove.

General color, *olive-green* (Ridgway, 1886, X, 18), sides of carapace *cream-color* (VI, 20). A *rufous* (IV, 7) spot on anterior margin of carapace. Lower side whitish. Anterior half of abdominal segments *hazel* (IV, 12). Chelæ *olive-yellow* (VI, 16), mottled with *olive-green.* Finger tips *orange* (VI, 3), followed proximally by a *citron-yellow* (VI, 15) band. One *rufous* articular tubercle above on the hand. Articular membranes of hand *lake-red* (VII, 2). Finger tips of chelæ of second and third pereiopods, and dactylopodites of fourth and fifth pereiopods *orange.* Pereiopods pale brownish-white, mottled and marbled with olive-yellow. Antennal flagellum annulated *olive-green* and *ochraceous* (V, 7). Spines on sides of carapace and rostrum *buff* (V, 13). Antennal scale *olive-yellow,* its center *olive-green.*

It is to be remarked that in this specimen no dark olive-green band is found near the finger-tips. The same was the case generally in specimens from Temple Creek, Albion, and from Elk Creek (all collected in autumn). However, specimens from Conneautville Station, Crawford County, collected in June, generally had a dark green, almost black band, succeeding the pale band. A similar dark band appeared in some of the Temple Creek specimens, after they had been preserved for some time in alcohol, but it disappeared again with the progress of the bleaching action of the preserving fluid. In collecting the specimens of this species and of *C. obscurus* in Erie County in October, 1904, I was generally able to distinguish the two species, where they were found associated, by the color of the finger tips. However, too much reliance should not be placed upon this character, since I was not subsequently able to test this observation.

The description of this species, as given above, is drawn from sixty-one specimens preserved in the collection of the Carnegie Museum. Of these, fifty-three are from the State of Pennsylvania (forty-eight from streams flowing into Lake Erie, five from the lake itself). One specimen is from Lake Erie, Erie County, Ohio, and seven are from the northern parts of Michigan.

DISTRIBUTION (see Plate XLII, Fig. 3).

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

Pennsylvania: *Erie County,* Lake Erie, Presque Isle, (D. A. Atkinson coll.); Lake Erie, Miles Grove; Walnut Creek, Swanville; Elk Creek, Girard; Elk Creek, Miles Grove; Conneaut Creek, Albion; Temple Creek, Albion; *Crawford County,* tributary of Conneaut Creek, Conneautville Station.

Ohio: *Erie County,* Lake Erie, Cedar Point, near Sandusky, (O. E. Jennings coll.).

Michigan: *Emmet County,* Crooked Lake, Oden near Petoskey, (E. B. Williamson coll.).

PREVIOUS RECORDS.[9]

Type locality: Oswego, Oswego County, New York, (Girard).[10]

CANADA: Montreal, Quebec, (Faxon); Toronto, Ontario, (Faxon).

NEW YORK: *St. Lawrence County*, Grass River, (Hagen); Canton, (Faxon); Black Lake, (Faxon); Ogdensburg, (Faxon); *Jefferson County*, Garrison Creek, Sackett's Harbor, (Girard); *Oneida County*, Oneida Lake, (Hagen); *Cayuga County*, Cayuga Lake, (Faxon); *Monroe County*, Rochester, (Hagen); *Niagara County*, Niagara-(Hagen); *Chautauqua County*, Forestville, (Faxon).

OHIO: *Lorain County*, Lake Erie, (Ortmann); *Ottawa County*, Portage River, Oak Harbor, (Faxon).

MICHIGAN: *Wayne County*, Detroit River, (Faxon); Northville, (Faxon); Ecorse, (Faxon); *Washtenaw County*, Ann Arbor, (Faxon); *St. Clair County*, St. Clair River, (Faxon); *Calhoun County*, Marshall, (Faxon); *Allegan County*, Otsego, (Faxon); *Saginaw County*, Saginaw River, (Faxon); *Charlevoix County*, Lake Michigan, Round and Pine Lakes, Charlevoix, (Ward).[11]

INDIANA: *De Kalb County*, Waterloo, (Hay); *Noble County*, Rome City, (Bundy); *Kosciusco County*, Turkey Lake, (Hay); *Marshall County*, Maxinkuchee Lake, (Hay); Twin Lakes, (Hay); *Laporte County*, Michigan City, (Faxon); *Carroll County*, Delphi, (Hagen); *Tippecanoe County*, Lafayette, (Faxon); *Marion County*, Indianapolis (Faxon); Irvington (Hay); Millersville (Hay); *Franklin County*, Brookville (Hay); *Brown County*, Salt Creek (Hay); *Monroe County*, Clear Creek, Bloomington (Faxon); *Greene County*, Switz City (Faxon); *Sullivan County*, Turman Creek (Faxon).[12]

ILLINOIS: *Macon County*, Decatur (Faxon); *McLean County*, Normal (Forbes); *Tazewell County*, Pekin (Forbes); *Kane County*, Geneva (Faxon); *Ogle County*, (Hagen); *Stephenson County*, Freeport (Forbes).[13]

WISCONSIN: *Greene County* (Faxon); *Dane County*, Madison (Faxon).

IOWA: *Scott County*, Davenport (Faxon); *Wapello County*, Ottumwa (Faxon).

New locality, not represented in Carnegie Museum: Spencerport, Monroe Co., New York, (Mus. Oberlin).

---

[9] I have omitted "Lake Superior" (Hagen), as unconfirmed (see Ortmann, 1905*b*, p. 132), and "Green River, Edmonson County, Ky." (Hay, 1802*a*, p. 235), as doubtful, being founded upon young specimens only.

[10] This is the first locality given by Girard, and consequently is the type locality.

[11] Faxon gives also from "Michigan": "St. Mary's Lake"; "Mouth of Battle Creek"; and "Lake Douglass." I have not been able to locate these.

[12] Faxon gives in addition: "White River, Indiana" (southeastern section, tributary to Ohio.)

[13] Faxon gives also: "Aux Plains River, Illinois," which I have not been able to locate.

REMARKS.

Cambarus propinquus in Pennsylvania belongs to Lake Erie and its drainage. The range being rather restricted, the material at hand is not very rich, and its study does not promise many results as to variation. Nevertheless there are a few striking facts, which may be mentioned. In the first place one of the chief specific characters, the longitudinal keel of the rostrum, is decidedly variable. All specimens at hand from outside of the state (eight) show a keel plainly, but this is not so with the Pennsylvanian specimens. The keel in these is often distinct, but shows a tendency to disappear. This is chiefly the case in young individuals, where the rostrum is comparatively narrower, the marginal spines are sharper, and the acumen is slenderer than in older individuals.

The armature of the chelipeds is also rather variable. There is always a strong spine in the middle of the inner margin of the carpopodite, and invariably a small tubercle anterior to it, which in young specimens is often spiniform. Sometimes there is also a small tubercle at the proximal end of the inner margin, but I have generally found this only in larger individuals. The lower side of the carpopodite, as a rule, has only one spine, located at the articulation with the hand, and this is present in all Pennsylvanian specimens I have seen. The anterior margin is often without any spine, or even tubercle; there is, however, a low tubercle developed in many cases, and in two cases it was spiniform, viz., in a male (second form) from Elk Creek, Miles Grove, and in a female from Presque Isle. Both of them had a distinct keel on the rostrum, so that they undoubtedly belong to this species. The rows of spines on the lower margin of the meropodite are generally represented by only two spines, the distal spine of each row being alone present. But it is remarkable that in the set from Conneautville Station, composed of twelve individuals, ten show an increase of the spines of the inner margin, from four to eight little teeth being present behind the large distal spine, while in eight specimens an additional smaller spine is found behind the distal spine of the outer margin. In every case this occurs only on one side, while the other side is normal. A similar increase of the number of spines of the meropodite is also to be observed in a few specimens from Temple Creek, Albion, in the two specimens at hand from Elk Creek, Miles Grove, in the female from Presque Isle, mentioned above, and in the specimen (female) from Sandusky, Ohio. Since the latter has also a spine on the anterior margin of the lower side of the carpopodite, the tendency to develop additional spines may extend simultaneously to carpopodite and meropodite.

The set of seven specimens from northern Michigan is remarkable for the fact that in no case is there a spine on the carpopodite at the lower articulation with the hand, but only a tubercle; in other respects they are typical, with a spine and anterior tubercle on the inner margin of the carpopodite, a low tubercle at the anterior margin of the lower side of the carpopodite, and only two spines on the lower margin of the meropodite.

In the shape of the sexual organs of the male there is much uniformity in their length and the shape of the tips. However, there is a tendency in the Pennsylvanian specimens toward the development of a slight notch on the anterior margin in the place where *C. obscurus* has a shoulder. I have only twelve males of the first form from Temple Creek, Albion, four from Walnut Creek, and two from Elk Creek. Of these, six from Temple Creek and one from Walnut Creek show a notch, while all the rest (eleven) have no trace of it. The notch never assumes the shape of the "shoulder" of *C. obscurus*, and the sexual organs differ in other respects from the later species, chiefly in that the tip of the inner part is never blunt or dilated.

The female annulus is rather constant, as has been said above; only slight differences due to age are noticeable.

We may sum up the variations of *C. propinquus* in the state of Pennsylvania by saying that there is a distinct inclination toward *C. obscurus*, indicated by the tendency of the rostral keel to disappear, of the chelipeds to increase in spinosity, and of the male copulatory organs to develop a notch at the anterior margin. Nevertheless there are numerous specimens which represent the typical *C. propinquus*. This fact is to be borne in mind, and we shall learn more about it when we come to discuss the geographical distribution of this and the related forms.

I introduce here the systematic account of a variety of this species, which is extralimital to the state of Pennsylvania. I have, however, decided to treat of it more fully, since its relation to the representative Pennsylvania form is highly interesting, and since we shall have to refer to it repeatedly in the chapter on distribution.

2*a*. Cambarus (Faxonius) propinquus sanborni (Faxon).

Cambarus sanborni Faxon, 1884*b*, p. 128.

Cambarus propinquus sanborni Faxon, 1885*a*, p. 91, Pl. 5, f. 3, Pl. 9, f. 10; Underwood, 1886, p. 372; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20, 48; Hay, 1899, p. 960, 964; Ortmann, 1905*b*, p. 132.

According to Faxon, this variety differs from the typical *C. propinquus* in the following characters: 1) The two parts of the male sexual organs are less deeply separated, and the tips are closer together. 2) The rostrum is not carinate. 3) The hands are finely pubescent. 4) The inferior median anterior spine of the carpopodite is evident.

I possess five specimens (obtained by exchange from Oberlin College) from one of the two localities originally mentioned by Faxon for this form (Oberlin, Ohio), which agree well with his account, with the exception that the pubescence of the hands is not developed; there are, indeed, a number of short hairs in some, chiefly the younger, specimens, implanted in the punctures, but such are also very frequently present in *C. propinquus* (as well as in *C. obscurus*). These hairs are generally present in new, recently moulted specimens, but wear off with age.

The male copulatory organs are very similar in shape to Faxon's figure, although they vary slightly with reference to the length of the separated tips. In this respect, however, the variety is closer to the typical form than to *C. obscurus*. In addition, I notice in the two males of the first form of this set that the inner part of the male organs, although it tapers to a point on a side view, is different on a posterior view. From behind it is broadly and bluntly rounded off, a fact which is due to a marked compression and flattening in an anteroposterior direction toward the tip. This is also the case in the male of the second form at hand. Here both tips of the sexual organs are blunt, that of the inner part less so than that of the outer. I cannot see that the tips of the male organs, either in the first or in the second form, are closer together than in *C. propinquus*.

The armature of the chelipeds in these specimens is slightly different from that of the typical *C. propinquus*, although similar variations have been observed in the latter. In all five specimens there are two distinct spines on the lower side of the carpopodite, one at the articulation with the hand, the other on the anterior margin. The inner margin of the carpopodite, besides the one strong spine, has a distal and a proximal tubercle, and in the two largest individuals (male and female) there are a few additional tubercles on the upper surface of the carpopodite. The inner lower margin of the meropodite invariably has in these specimens behind the distal spine a row of small teeth, becoming spiniform in the larger individuals. The number of teeth in this row is from six to eight. In two specimens the outer lower margin possesses a small tubercle behind the distal spine of each cheliped. In one specimen there is only a tubercle on the right side, and two others have only the distal spine.

In addition to the above specimens from Oberlin I have seen among the Oberlin collections other specimens from the state of Ohio, and have myself collected in eastern Ohio and northern West Virginia a number of specimens, which undoubtedly belong to the same form. The characters are practically the same, and only a few remarks are necessary.

1. The keel of the rostrum is invariably lacking. There is not a single individual which shows any trace of it.

2. The hand of the adult male of the first form has a distinct tendency to become broader than in the typical *propinquus.* This is well shown in the largest male from Oberlin. However, this may be due to the fact that the specimens of this variety at hand are larger than those of the typical form. I notice, however, in specimens from the Tuscarawas drainage and from West Virginia, a tendency in old specimens, chiefly males, to develop on the upper surface of the hand, near the double row of tubercles of the inner margin, additional low tubercles. These may be scattered over the inner half of the surface, or a few of them (3–5) may form an indistinct row between the upper articular tubercle with the carpopodite and the articular tubercle with the dactylopodite. This is a distinct approach toward *C. obscurus,* where similar tubercles are present in larger individuals.

3. The two spines of the lower side of the carpopodite are almost always well developed. There are a number of specimens where they are only bluntly spiniform, or even tubercular, but this is apparently due to wear, a large number of the specimens at hand having been collected in spring, and possessing old worn shells, which had gone through the winter. In a few cases the tubercle on the anterior margin is barely indicated, but all these are cases of regenerated chelæ, as indicated by their size. The armature of the inner margin of the carpopodite entirely corresponds to the Oberlin specimens, old specimens developing additional tubercles on the upper side. A large female from Middle Island Creek, W. Va., has on the left carpopodite a small, but sharp, accessory spine behind the large median spine.

4. The armature of the meropodite is similar to the Oberlin specimens. There is always a series of small teeth behind the anterior spine of the inner lower margin (in old shells they may be indistinct, due to wear); the outer lower margin has an anterior spine, and often a tubercle or a small spine behind it. The latter is very frequent in specimens from the Tuscarawas basin, while in those from the tributaries of the Ohio in West Virginia it is rare; nevertheless, in the large female from Middle Island Creek this second spine is very prominent on the left meropodite.

5. The male copulatory organs are of the *propinquus*-type, that is to say, without a shoulder. There is, however, a distinct tendency, not noticed in the Oberlin specimens, to develop at the anterior margin a small notch in the male of the first form, and it seems that this tendency increases in specimens taken toward the south. Out of ten males of the first form collected at Canton, Ohio, five have no trace of this notch, two have a slight curve in its place, and three show it clearly. This notch in these cases never assumes the shape of a "shoulder." In specimens from Conotton Creek in Harrison and Carroll Counties, Ohio, (only a few males of the first form are at hand), no notch was observed. But out of thirteen males of

the first form collected in Fishing Creek, West Virginia, only two had no trace of it; six had a curve developed in its place, and in five others it was distinct, in one or two representing a blunt angle. The length of the tips of this organ varies slightly, but it is generally less than in *C. obscurus.* The tip of the inner part always corresponds to that of the Oberlin specimens, being compressed and rounded off.

6. The annulus of the female is always of the *propinquus*-type, that is to say, flat, with no tubercles. In old females it becomes a little uneven, the anterior and posterior parts being slightly swollen, but there are never two distinct tubercles as is the case in *C. obscurus.*

We may condense the varietal characters of this form as follows:

C. propinquus sanborni clearly is nearer to *propinquus* than to *C. obscurus* on account of the lack of a distinct shoulder on the anterior margin of the copulatory organs of the male of the first form, on account of the general shape and size of this organ, and further, on account of the flat female annulus. It differs from *C. propinquus* in the flattened and rounded tip of the inner part of the male organ, in the lack of a median keel on the rostrum, and in the shape and armature of the chelipeds, although the latter differences are slight and not always reliable. Just in the latter characters, and in the tendency to develop a notch on the anterior margin of the male organ, it inclines toward *C. obscurus.* Thus it is clearly a transitional form toward *C. obscurus* of western Pennsylvania, and its geographical distribution, as we shall see below, is also intermediate between *C. propinquus* and *C. obscurus.*

The *colors* of *C. sanborni* agree throughout with those of *C. propinquus* and *C. obscurus.* The color of the newly laid eggs is dark olive-green, sometimes almost black.

There are one hundred and sixteen specimens of this variety at hand; five are from the Lake Erie drainage in northern Ohio; eighty-one from the Tuscarawas drainage in eastern Ohio, and thirty from Fishing and Middle Island Creeks in West Virginia.

DISTRIBUTION.

(See Plate XLII, Fig. 3.)

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

OHIO: *Lorain County,* Waterworks Reservoir, Oberlin (R. L. Baird coll., exch. Mus. Oberlin); *Stark County,* West Branch of Nimishillen Creek, Canton; *Carroll County,* Conotton Creek, New Hagerstown; *Harrison County,* Conotton Creek, Bowerstown; *Tuscarawas County,* Dennison (V. Sterki coll.).

West Virginia: *Wetzel County*, Fishing Creek, New Martinsville; *Pleasants County*, Middle Island Creek, St. Marys.

PREVIOUS RECORDS.

Type locality: Smoky Creek, Carter County, Kentucky (Faxon).

Ohio: *Lorain County* (Faxon); Vermilion River; Beaver Creek; French Creek (Ortmann); *Wayne County*, Killbuck Creek, Creston (Ortmann); *Tuscarawas County*, Tuscarawas River, Gnadenhütten (Ortmann); *Knox County*, Big Jelloway Creek (Osburn and Williamson); *Licking County* (Williamson); *Franklin County*, Alum Creek (Osburn and Williamson).

3. Cambarus (Faxonius) obscurus Hagen.

(Plate A, Fig. 1 and 2; Plate XXXIX, Fig. 7*a*–7*e*; Plate XL, Fig. 1.)

Cambarus obscurus Hagen, 1870, p. 69, Pl. 1, f. 72–75, Pl. 3, f. 154; Smith, 1874, p. 639; Faxon, 1884*b*, p. 148; Faxon, 1898, p. 652; Ortmann, 1905*a*, p. 402.

Cambarus propinquus obscurus Faxon, 1885*a*, p. 92; Faxon, 1885*b*, p. 360; Underwood, 1886, p. 372; Hay, 1899, p. 960, 964.

Cambarus propinquus and *C. rusticus* Williamson, 1901, p. 13.

Cambarus (*Faxonius*) *obscurus* Ortmann, 1905*b*, p. 112.

Body of the same shape as in *C. propinquus*, but slightly more robust in old specimens.

Carapace similar to *C. propinquus*, but the width of the hepatic, as also of the branchial regions, is slightly greater; $G:H:B = 1:1.1:1.3$ to 1.5. These differences of dimension may, however, be due to the fact that large individuals of this species are at hand.

Cervical groove and *areola* identical with those of *C. propinquus*, but the areola generally is slightly longer than half of the anterior section of the carapace.

Rostrum similar to that of *C. propinquus*, but always without any trace of a median keel. In young specimens the rostrum and its acumen are about identical in shape with those of *C. propinquus*. In older specimens there is a tendency to a shortening of the acumen, which often reaches only to the distal end of the second joint of the peduncle of the antennula and to the base of the terminal joint of the peduncle of the antenna. The marginal spines in old individuals are often very small and indistinct, represented by mere angles. The postorbital ridges are as in *C. propinquus.*

The punctures and spines of the carapace are identical with those of *C. propinquus.*

The *abdomen, epistoma, antennula,* and *antenna* are also similar to those of *C. propinquus.*

The *first pereiopods* (Plate XL, Fig. 1) are generally more robust than in *C. propinquus,* particularly in adult males. Hand wider and more distinctly depressed. The fingers more widely gaping in old males, and the S-shaped curve of the movable finger more pronounced ; in old females there is also a slight gap at the base of the fingers. The upper surface of the hand possesses, particularly in large specimens, a small number of scattered low tubercles near the inner margin, and very often (but not always) there is a row of 3–5 tubercles running toward the base of the movable finger, parallel to the inner margin. Tubercles of the outer margin of the dactylopodite more pronounced. The sculpture of the hand is rather variable, and most distinctly developed in old males. The shape of the hand is rather different in the male and female ; in the female the fingers are shorter, less gaping (or not at all), rendering the outline of the hand more regularly ovate. (See Plate A, Figs. 1 and 2.)

The *carpopodite* differs from that of *C. propinquus* in the development of a strong tubercle on the anterior margin of the lower side. This tubercle very rarely is indistinct (chiefly so in regenerated claws) ; generally it ends in a distinct, stout, conical spine. On the inner margin and on the upper face additional low tubercles are not infrequently found.

The *meropodite* differs from that of *C. propinquus* by the constant presence of a series of 4–8 small tubercles, or teeth, behind the distal spine on the inner lower margin. These teeth are never wanting in any of my specimens. The outer lower margin has one or two spines. The latter number is comparatively rare. In regenerated claws very often there is no spine at all on the inner lower margin.

The other characters of the pereiopods are similar to those of *C. propinquus.*

The *first pleopods* of male of the first form (Plate XXXIX, Figs. 7*a* and 7*b*) are of the general type of those of *C. propinquus*, but slightly longer, reaching to the anterior margin of the coxopodites of the third pereiopods. The inner part does not gradually taper to the tip, but is of nearly uniform thickness, with the tip rounded off and slightly compressed in the antero-posterior direction. Sometimes the tip is even slightly thickened. The anterior margin of this organ, at a point somewhat below the separation of the two parts, has a rather sharp, well marked shoulder, which is absent in none of the specimens at hand (several hundred).

In the male of the second form (Plate XXXIX, Fig. 7*c*) this shoulder is missing, and the inner part is blunt, similar in shape to the male of the first form, and not tapering to a point as in the typical *C. propinquus.*

The *annulus ventralis* of the female has the general shape of that of *C. propinquus,* but the depression in the middle is well marked, and the anterior part has two distinct, subconical tubercles. The posterior part is also elevated into a flat and low tubercle. These tubercles are less distinct in young specimens, but always well developed in females of medium and large size.

Size. — Hagen gives the length as 3.5 in. = 89 mm. The largest individual at hand is a female from Pucketta Creek, Allegheny County (Atkinson coll.), which measures 93 mm. in length. The largest male of the first form is from the Ohio River at Neville Island, Allegheny Co., which is 86 mm. in length. Individuals over 80 mm. in length are not rare in the larger rivers.

Colors (Plate A, Figs. 1 and 2). —The colors of this species are identical with those of *C. propinquus.* In fresh specimens the general ground color is light *olive-green* (Ridgway, 1886, X, 18), with darker spots in young specimens; in older individuals it is rather *tawny-olive* (III, 17). On the branchial region there is an oblique band of *cream-color* (VI, 20), edged by *olive-green* near the margin of the carapace, which is again *cream-color.* This cream-color in very brightly colored specimens sometimes becomes *primrose-yellow* (VI, 13). On the anterior margin of the carapace below the eyes there is a spot which may be *rufous* (II, 7), *ochraceous-rufous* (V, 5), edged with *sulphur-yellow* (VI, 14), *ochre-yellow* (V, 9), or *primrose-yellow* (VI, 13). The abdomen is *olive-green* or *tawny-olive,* shading into *chestnut* (IV, 9) on the anterior margins of the segments. There are one (sometimes two) median and two lateral rows of dark *olive-green* patches. The chelæ are light *olive-green,* shading distally into *olive-yellow* (VI, 16). The finger-tips are *orange-buff* (VI, 22), *orange* (VI, 3), or *raw sienna* (V, 2), followed by a pale, and a *dark green,* sometimes *almost black* band. The latter is not always present. The upper surface of the hand at the base of the dactylopodite has two (rarely one) *rufous* or *ochraceous-rufous* (V, 5) articular tubercles. The tubercles of the hand are *buff-yellow* (VI, 19) or *buff* (V, 13). The articular membranes of the hand are *wine-purple* (VIII, 15). The legs are *olive-yellow* (VI, 16) and whitish, with *olive-green* on upper edges.

The above colors fade in old specimens, and are often obscured by blackish or brownish coats of dirt. A variety with the chelæ and anterior parts of the carapace of a pale dirty bluish color was repeatedly observed in the Alleghany River at Sandy Creek and Twelve Mile Island, but only old specimens of this form were found. Young specimens generally vary more toward green, old ones toward tawny or brown.

The color of the newly laid eggs ranges from *sage-green* (X, 15) to dark *olive-green* (X, 18), or often to *almost black.* When somewhat advanced in development, the egg becomes in part *prune-purple* (VIII, 1), in part *cream-color* (VI, 20), or whitish.

Of this species, seven hundred and twenty-one specimens are at hand. Most of them (six hundred and sixty-two) are from the state of Pennsylvania; fifty-seven are from the "Panhandle" of West Virginia, and two from Maryland (Wills Creek, Ellerslie). Many others have been collected, but no record has been kept, since they were used for exchange, dissection, and experiment.

DISTRIBUTION.

(See Plate XLII, Figs. 2 and 3.)

LOCALITIES REPRESENTED IN THE COLLECTIONS OF THE CARNEGIE MUSEUM.

PENNSYLVANIA: *Greene County*, Pennsylvania Fork of Fish Creek, Deep Valley; Smith Creek, Waynesburg; Bates Fork, Deer Lick; Pumpkin Run, Rice's Landing; *Fayette County*, Cheat River, Cheat Haven; Youghiogheny River, Connelsville; *Washington County*, Buffalo Creek, Taylorstown; Harmon's Creek, Dinsmore; Raccoon Creek, Burgettstown; Pigeon Creek and Taylor's Run, Monongehela City; *Beaver County*, Beaver (S. N. Rhoads coll.); Raccoon Creek (Atkinson, Williamson and Todd coll.); Little Beaver Creek, New Galilee (A. Kœnig coll.); Brady's Run, Fallston; Ohio River, Baden; Ohio River, Ambridge; *Lawrence County*, Eckles Run, Wampum; Big Run, Newcastle (D. C. Hughes coll.); *Mercer County*, Otter Creek, Mercer; Shenango Creek, Hadley (O. E. Jennings coll.); *Crawford County*, Shenango River, Linesville; Shermansville (O. E. Jennings coll.); Conneaut Outlet (D. C. Hughes coll.); Oil Creek, Spartansburg; *Erie County*, Conneaut Creek, Albion; Elk Creek, Miles Grove; French Creek, Union City; *Butler County*, Tributary of Slippery Rock Creek, Branchton; Thorn Creek, Renfrew; Rough Run, West Winfield; *Allegheny County*, Ohio River, Neville Island; Ohio River, Bellevue (E. Hays and R. Taylor coll.); Ohio River, Shoustown; Flaugherty Run, Moon Township (Q. T. Shafer coll.); Chartiers Creek, Carnegie (D. A. Atkinson coll.); Chartiers Creek, Bridgeville (D. A. Atkinson coll.); Turtle Creek, Pitcairn (D. A. Atkinson coll.); Youghiogheny River, Boston (D. A. Atkinson coll.); Crystal Lake, Pittsburgh (D. A. Atkinson coll.); Girty's Run, Millvale; Stone Run, Thornhill; Pine Creek, below Bakerstown Station (D. A. Atkinson coll.); Alleghany River, Six Mile Island, (S. N. Rhoads and E. B. Williamson coll.); Squaw Run, Aspinwall; Alleghany River, Sandy Creek; Alleghany River, Verona (D. A. Atkinson coll.); Alleghany River, Twelve Mile Island; Deer Creek, Harmarville; Little Deer Creek, Russelton; Pucketta Creek (D. A. Atkinson coll.); Little

Bull Creek, Tarentum (A. Kœnig coll.); Alleghany River, Butler Junction; *Westmoreland County,* Kiskiminetas River, Livermore; Conemaugh River, Blairsville Intersection; Reservoir of McGee Run, Derry; Whitethorn Creek, Dundale; small tributary of Loyalhanna River, New Alexandria; Loyalhanna River, Ligonier; Loyalhanna River, Crisp; *Indiana County,* Two Lick and Yellow Creeks, Homer; Crooked Creek, Creekside; Little Mahoning Creek, Goodville; *Armstrong County,* Long Run, Avonmore Station; Alleghany River, Kittanning; Alleghany River and Pine Creek, Mosgrove; Alleghany River, Templeton; *Clarion County,* Alleghany River, Red Bank; *Jefferson County,* Pond at Punxsutawney; *Clearfield County,* Sandy Lick Creek, Du Bois; *Venango County,* Alleghany River, Franklin; Oil Creek, Oil City; *Forest County,* Alleghany River, Tionesta; *Warren County,* Brokenstraw Creek and Crouse Run, Garland; *McKean County,* Alleghany River, Larabee; *Bedford County,* Wills Creek, Hyndman.

WEST VIRGINIA: *Hancock County,* Harmon's Creek, Holidays Cove; *Brooke County,* Harmon's Creek, Colliers; *Ohio County,* Wheeling Creek, Elm Grove; *Marshall County,* Wheeling Creek, Union Township; Grave Creek, Cameron; Pennsylvania Fork of Fish Creek, Nuss; *Wetzel County,* Fishing Creek, New Martinsville.

MARYLAND: *Alleghany County,* Wills Creek, Ellerslie.

PREVIOUS RECORDS.

Type locality: New York, Monroe County, Genessee River, Rochester (Hagen),

NEW YORK: *Cattaraugus County,* Alleghany River, Salamanca (Ortmann).

PENNSYLVANIA: *Westmoreland County* (Faxon); *Allegheny County* (Williamson); *Warren County,* Alleghany River, Corydon (Ortmann).

ADDITIONAL LOCALITIES.

Material in the Department of Agriculture, Harrisburg, collected by W. R. McConnell. — Shenango River, Jamestown, Mercer County; French Creek, Franklin, Venango County; small stream and pond, below Indiana, Indiana County; Branch of Genessee River, Ulysses, Potter County.

Alleghany River, Montrose, Allegheny County, Pa. (collected by the writer, but material used for study); Indian Creek, Jones Mills, Westmoreland County, Pa., (seen by the writer);[14] Harmon's Creek, Hanlan, Washington County, Pa. (seen by the writer); Ohio River, Congo, Hancock County, W. Va., (seen by the writer).

---

[14] This locality was discovered in the beginning of the investigation by the writer, and since its importance was then not understood, no specimens were preserved; but the record is absolutely trustworthy.

REMARKS.

Cambarus obscurus is the river species of the Upper Ohio drainage. It is widely distributed in western Pennsylvania. Compared with the allied species *C. propinquus*, which occupies a much wider area, it is rather uniform in its characters all over its known range. It nowhere reveals a tendency to vary in the direction of *C. propinquus*, or of *propinquus sanborni*. This is the more remarkable because *C. propinquus* distinctly inclines toward this species in Erie and Crawford Counties, (in the lake drainage), and likewise because *C. propinquus sanborni* shows such a tendency in Wetzel County, West Virginia.

The variations observed in our abundant material have been briefly indicated above. However, it deserves special mention that the specific characters are scarcely subject to any variation.

Very interesting conditions are offered by the spines of the outer lower margin of the meropodite of the cheliped. One or two spines may be present, the proximal one smaller and often represented only by a small tubercle. Looking over our material, I find that only one spine is present in all individuals from the upper Alleghany drainage, including all the tributaries from Red Bank Creek northward (sixty-one specimens are at hand). In Armstrong, Indiana, Westmoreland, and Allegheny Counties, in the drainage of the Alleghany River, and in the whole drainage of the Monongahela, the Beaver, and Ohio proper, a second spine may be present, but such cases are not frequent, and generally this spine is found only on one of the two chelipeds. There is a tendency of this character, more frequently displayed in the southwestern extremity of the range. Two such spines on either side (right and left) are very rare, and I have found them only in twenty specimens; fifteen of which belong to the Ohio drainage: two to that of the Monongahela, six to that of the Beaver, and seven to that of the Ohio below Beaver. Two cases were discovered in Wills Creek, Maryland, and three in Conneaut Creek at Albion, Erie County, Pa.

The latter specimens are interesting inasmuch as in Erie and Crawford Counties two drainage areas come together with that of Lake Erie, namely, that of the Shenango River, a tributary of the Beaver, and that of French Creek, a tributary of the Alleghany. In the latter creek and its tributaries I have never seen an individual with two spines (seventeen specimens are at hand). Among the material from the Beaver River drainage (fifty-six specimens) there are twenty-one with two spines. Thus the tendency to develop two spines is markedly present in the drainage of the Beaver, while it is apparently absent in French Creek.

The specimens from the Lake Erie drainage in Conneaut Creek quite often have two spines (eight specimens out of twenty-two); and thus correspond to the Beaver River form, and to those from Elk Creek, in which one specimen out of six has two spines. Thus it appears that the form in the drainage of Lake Erie more closely approaches the form found in the Beaver River than that found in French Creek, although it must be granted that the material at hand seems to be not entirely satisfactory, being somewhat too scanty from French Creek, and decidedly insufficient from Elk Creek.

A few freaks have come under observation in the following cases:

1. As has been said, the rostrum reveals in old individuals a tendency to a shortening of the acumen. The extreme is reached in a specimen (male of the first form) 74 mm. long, from Conneaut Outlet, Crawford County (D. C. Hughes coll.), where the acumen is broadly triangular and hardly longer than the short marginal spines, reaching only to the distal end of the basal joint of the peduncle of the antennula. The acumen is well formed (not deformed), showing no traces of injury. But that this specimen undoubtedly has been injured at some time earlier in its life, is revealed by the fact that both claws are comparatively small, and by the characters of regeneration (lack of spines on the outer lower margin of the meropodite, the absence of a tubercle on the anterior margin of the lower side of the carpopodite, and the generally weak and slender shape).

2. A female (46 mm. long) from Brokenstraw Creek, Garland, Warren County, has the acumen of the rostrum directed obliquely to the left side, and the right margin of the rostrum has five marginal spines. This seems to be due to an injury received in earlier life. The left claw is also smaller and of the regenerated type.

3. A specimen (55 mm. long) from the Alleghany River at Sandy Creek (collected by the writer, Nov. 19, 1904, Cat. No. 74. 479), has the characters of a female in the shape of the chelæ and the lack of hooks on the pereiopods. The annulus ventralis, however, is very indistinct, although its outlines and slight median depression are visible, as is also the median fissure. But this individual has the male genital opening in the coxopodite of the fifth pereiopod, and the first pleopod is of the male type, although small; it is unusually short, reaching only to the anterior margin of the coxopodites of the fourth pereiopods; it is of the type of the first form, with a distinct shoulder; the outer part is horny and distinctly longer than the inner part. The second pleopods are entirely of the male type. According to the sexual orifice and the copulatory organs, we are to regard this as a male with certain female characters.

4. A pendant to the last specimen is one (67 mm. long) from the Ohio River,

Neville Island, (collected by D. A. Atkinson, May 14, 1899, Cat. No. 74. 36). The claws are intermediate between male and female, but inclining toward the male form. The third pereiopods have strong and well developed hooks on the ischiopodites of the type of the first form male. The first pleopods are very peculiar, (Plate XXXIX, Figs. 7*d* and 7*e*), and unlike those of *C. obscurus;* they rather resemble those of *C. limosus.* Their length and strength are normal, but there is no shoulder, and the two parts are separated only for a short distance at the tips, similar to *C. limosus*, but the tips are not twisted. The outer tip is horny and pointed, the inner soft, thicker, and tapers to a blunt point. The second pleopods are of the normal male type. In addition this individual possesses a well developed annulus ventralis, and sexual orifices only on the third pereiopods. Thus it appears to be a female, with the secondary sexual characters of the male well, but not specifically, developed.

None of the two cases of apparent hermaphroditism just described (Nos. 3 and 4) agrees with any of the four cases mentioned by Faxon, (1885*a* p. 13, 14), or the four described by Hay, (1905, p. 226 and 227). Additional cases will be described below under *C. bartoni.* There is in the Carnegie Museum a further individual of hermaphroditic character, namely a specimen of *Cambarus rusticus* Girard, from the Wabash River, Bluffton, Indiana, collected by Mr. E. B. Williamson, June 1, 1905, Cat. No. 74. 578. I append a description of it.

The specimen is externally a female, possessing the female type of claws, a well-developed annulus, female sexual openings, and no hooks on the third pereiopods. But the first pleopods are peculiar; they are short and stout; the bases are identical with those of the male pleopods; the distal parts, however, reach only to about the middle of the coxopodites of the fourth pereiopods; their tips are soft, blunt, and slightly curved inward, and possess the furrow which divides them into an outer and inner part, but these parts are not separated at the tips. The second pleopods are of the female type. This case corresponds in a certain degree to the second, third, and fourth, mentioned by Faxon, chiefly so to the third (in *C. diogenes*). The specimen is apparently a normal female, only the first pleopods are transformed in a peculiar way, resembling the male type generally, but differing from the specific shape. In the present case the first pleopod is different from Faxon's case in detail.

4. CAMBARUS (BARTONIUS) BARTONI (Fabricius).

(Plate B, Fig. 1; Plate XXXIX, Fig. 1*a*–1*f*, and Fig. 8; Plate XL, Fig. 2.)

Astacus bartoni Fabricius, 1798, p. 407; Say, 1817, p. 167; Harlan, 1835, p. 230. f. 3; Gould, 1841, p. 330; Thompson, 1842, p. 170; De Kay, 1844, p. 22, Pl. 8, f. 25; Gibbes, 1850, p. 195, (partim).

Astacus ciliaris Rafinesque, 1817 p. 42.

Astacus pusillus Rafinesque, 1817, p. 42.

Astacus affinis Milne-Edwards, 1837, p. 332 (*non* Say).

Cambarus bartoni Girard, 1852, p. 88; Bell, 1859, p. 210; Hagen, 1870, p. 75, Pl. 1, f. 47–50, Pl. 2, f. 135–139, Pl. 3, f. 166; Abbott, 1873, p. 80; Smith, 1874, p. 639; Putnam, 1874, p. 191; Faxon, 1884*b*, p. 22; Faxon, 1885*a*, p. 59; Faxon, 1885*b*, p. 358; Underwood, 1886, p. 367; Ganong, 1887, p. 74; Faxon, 1890, p. 622; Hay, 1896, p. 487, f. 6; Faxon, 1898, p. 649; Osburn and Williamson, 1898, p. 21; Williamson, 1899, p. 47; Hay, 1899, p. 959, 966; Williamson, 1901, p. 11; Ortmann, 1905*a*, p. 390; Paulmier, 1805, p. 134, f. 6; Rathbun, 1905, p. 18.

Cambarus pusillus and *montanus* Girard, 1852, p. 88.

Cambarus (*Bartonius*) *bartoni* Ortmann, 1905*b*, p. 120, 134.

Body robust, very sparsely pubescent in fresh, but perfectly naked in old specimens, with only a few hairs on the fingers of the chelæ, and sometimes a slight pubescence on the cutting edge of the fingers.

Carapace subovate, strongly depressed. $G:H:B = 1:1.3$ or $1.4:1.5$ or 1.6. Greatest width of branchial regions well forward, at a short distance behind the cervical groove. Upper surface of carapace very flat.

Cervical groove deep, not interrupted on the sides. *Areola* distinctly longer than half of the anterior section of carapace; $a:p = 1:0.6$ Areola rather broad ($w:l = 1:5$ or 6), with about 3–5 irregular rows of punctures.

Rostrum (Plate XXXIX, Fig. 1*a*–1*f*) broad and short, reaching generally to the distal end of the second joint of the peduncle of the antennula, and hardly beyond the middle of the fourth joint of the peduncle of the antenna. Upper surface almost flat or only slightly concave, but margins elevated, without marginal spines. The margins converge more or less from the base, sometimes they are almost parallel, and near the apex they are suddenly contracted into a short, triangular acumen having a sharp point. The angles at the base of the acumen are rounded, but generally well marked, and the elevated margins are continued to the apex, although slightly decreasing distally from the lateral angles. Postorbital ridges short, almost parallel, angulated anteriorly, but without spine, except in young specimens.

Surface of carapace punctate, distinctly granulated on the hepatic region in larger specimens. There are also a few more or less distinct granulations immediately behind the cervical groove, but no spine. External orbital angle well marked by an angulation or a small tubercle, more rarely, and only in young specimens, spiniform. Branchiostegal spine formed by a small tubercle, which is sometimes obsolete.

Abdomen as long as carapace, or slightly shorter or longer; it is slightly wider in the female than in the male, but hardly wider than the carapace in the former. Anterior section of telson on the posterior lateral corners generally with two, more rarely with three spines. Posterior section semi-elliptical, distinctly wider than long, slightly shorter than anterior section.

Epistoma with posterior part broad and short, about two and a half times as broad as long, with a distinct transverse groove on either side slightly posterior to the middle, and an anterior median depression. Anterior section constricted at the base, semi-circular, with a median anterior point. This point may be strongly developed, or almost entirely absent. Transverse diameter distinctly greater than the longitudinal.

Antennula with a small, often spiniform, tubercle on the lower margin of the basal joint.

Antennal peduncle with a tubercle on the outer side of the first joint, which is often spiniform, chiefly so in young specimens; second joint with or without a very indistinct tubercle.

Antennal scale short and narrow, slightly longer than the rostrum, reaching to, or almost to, the end of the fourth joint of the antennal peduncle. Spine of outer margin strong. Laminar part not much broader than the marginal spine.

Flagellum reaching to the anterior margin or to the middle of the telson in the male, slightly shorter in the female, but sometimes considerably shorter, without apparent trace of having been injured. In some cases it reaches only the middle of the second abdominal segment.

First pereiopods (Plate XL, Fig. 2) very strong and robust in old individuals, particularly males. Hand elongate-ovate, broad, and strongly depressed. Surface punctate. Inner margin of palm short, curved, with a single marginal row of more or less distinct, low tubercles. Outer margin smooth, rounded proximally, carinate distally. Fingers longer than palm, not gaping in young individuals, but with a wide gap at the base, meeting only at the tips, most noticeably in old males. Outer margin of movable finger punctate, or, in older specimens, with a few indistinct tubercles. Cutting edges with tubercles, larger in the proximal part. Upper surface of each finger with a low longitudinal rib, bordered by rows of punctures. This rib often becomes indistinct, especially on the movable finger in old males.

Carpopodite slightly longer than wide, shorter than palm, with a deep longitudinal sulcus above. Inner margin with a strong pointed or blunt spine, which is generally distinctly hooked, going off almost at a right angle, but curving forward in the distal part. A small spine or tubercle (sometimes double) may be added to it proximally. Lower surface with a blunt conical tubercle in the middle of the anterior margin (occasionally spiniform). The tubercle at the articulation with the hand is generally obsolete. There are sometimes additional tubercles; the one which most frequently occurs is a small spine or tubercle between the large one on the inner margin and that on the anterior margin of the lower side.

Meropodite smooth, with 1–3 tubercles near the distal end of the upper margin, one of which is often spiniform in young specimens; in old specimens they are generally very indistinct or wanting. Lower side with two rows of spiniform tubercles. The outer rows consist of 1–6 (very rarely only one tubercle). Six were found in only one instance, that of a regenerated cheliped. Generally there are two or three. The inner row has 6–11 spiniform tubercles, of which the distal is the largest. A small tubercle on the outer articulation with the carpopodite may be present or absent.

Ischiopodite of third pereiopod hooked in the male. The hook of the first form is strong and subconical.

The *coxopodite* of the fourth pereiopod in the male possesses a prominent rounded and compressed tubercle.

First pleopods of the male of the first form (Plate XXXIX, Fig. 8) stout and short, reaching to the posterior margin of the coxopodite of the third pereiopods. They are not articulated at the base. The two parts are separated at the tips for a short distance, and both are curved sharply backward, forming almost a right angle with the basal part. Distally they are partly twisted, so that the outer part is directly anterior to the inner. The outer part is horny, compressed, falciform, the tip pointed, with a small posterior accessory point (often worn off). The inner part is soft, swollen at the base, and suddenly tapering to a blunt point.

In the male of the second form this organ may be articulated at the base (in the case of the young) or not articulated (in older specimens). Both parts are separated distally for a short distance, and the outer part is soft, not horny, less distinctly compressed, and blunt. In the young these organs are considerably shorter than in older specimens.

Annulus ventralis of the female transversely rhombiform, with a deep central depression and a longitudinal S-shaped fissure. Anterior and more particularly the posterior margins elevated. The whole anterior portion of the annulus often appears depressed compared with the elevated posterior margin. Where the longitudinal fissure passes over the posterior margin the latter is slightly depressed. In young females the central depression is less marked, and the margins are consequently less elevated, giving a rather flat appearance on the annulus.

Size. — This species in western Pennsylvania reaches a considerable size, although the maximum recorded by Hagen (3.6 = 91 mm.) has not been observed. Faxon, (1885*a*, p. 64), mentions a specimen from the Mammoth Cave, Ky., measuring 108 mm., but this is not the typical form. The largest individuals in the Carnegie Museum are two females, the one from Braeburn, the other from Derry, Westmoreland County, both measuring 87 mm. in length. The largest male (first form) is from North Versailles Township, Allegheny County, and measures 83.5 mm.[15] In western Pennsylvania specimens over 80 mm. are not altogether rare.

In the eastern portions of the state this species is much smaller. The largest specimen at hand is a female from Roxboro, 67 mm. long, and a male (first form) from Manayunk, Philadelphia County, 66.5 mm. long, (both collected by H. Gera). Specimens over 60 mm. are not frequent in eastern Pennsylvania.

Colors. — Generally dull and not much varied, greener in young specimens, browner in old ones. (See Plate B, Fig. 1.)

The carapace and abdomen *olive-green* (Ridgway, 1886, X, 18) to *tawny-olive* (III, 17), *chestnut* (IV, 9), and *burnt umber* (III, 8), a shade darker dorsally, lighter on the sides. Margins of rostrum, in the browner specimens, *ferrugineous* (IV, 10). Distal third of finger *rufous* (IV, 7), or *tawny* (V, 1). Tubercles of the cutting edges of fingers *ochraceous buff* (V, 10). In brown individuals there is generally some green on the chelæ.

Aside from young individuals, where the normal olive-green prevails, this species shows a distinct tendency toward the brown and chestnut shades, more so than the river species, *C. limosus*, *C. propinquus*, and *C. obscurus.*

In some cases the colors are brighter. Individuals shading to a copper-color are not rare, and I have seen a few where a dirty slate-blue was the ground-color. Of course, as in other species, in old specimens the original colors are largely obscured by a deposit of mud, rendering the specimens sometimes almost black.

In very young specimens (10 to 20 mm. long) the color is olive-green, semitransparent, with the chelæ almost entirely ferrugineous.

The color of the newly laid eggs is almost black, with, or without, a purplish hue (*indian-purple,* VIII, 6). In a more advanced stage they become particolored: *prune-purple* (VIII, 1) or *dahlia-purple* (VIII, 2) on one side, *grayish* or *whitish* on the other.

The Carnegie Museum possesses seven hundred and fifty-five specimens of this species, six hundred and fourteen of which are from the state of Pennsylvania, nineteen from New York, ten from New Jersey, six from Ohio, seventy from West Virginia, thirty-four from Maryland, and three from North Carolina.

---

[15] The female from Hill, Westmoreland County, mentioned previously (Ortmann, 1905*a*, p. 391) is 85 mm., not 89 mm. as stated ; the male from Cheat River (*ibid.*) is not 92 mm., but 82 mm. in length.

DISTRIBUTION.

Localities represented in the collection of the *Carnegie Museum.*

PENNSYLVANIA: *Delaware County,* Dicks Run, Wallingford; *Philadelphia County,* Manayunk, (H. Gera coll.); Domino Lane Run, Roxboro, (H. Gera coll.); Wissahickon; *Bucks County,* Grenoble; Dark Hollow Run, New Hope; *Northampton County,* Bushkill Creek, Easton, (A. E. Davison coll.); *Lehigh County,* Little Lehigh Creek, Emaus; *Montgomery County,* West Manayunk, (H. Gera coll.); *Bucks County,* Shoemakersville; *Chester County,* Valley Forge; *Lancaster County,* Pequea; *York County,* Arthur Run, York Furnace; *Dauphin County,* Susquehanna River, Halifax; *Northumberland County,* Georgetown; *Franklin County,* Dickey; Williamson; *Fulton County,* Dogtown; Big Cove Creek, McConnellsburg; *Blair County,* Frankstown Branch of Juniata River, Loop near Hollidaysburg; *Bedford County,* Bedford Springs (A. Koenig coll.); *Cameron County,* Sinnamahoning Creek, Driftwood; Sinnamahoning; *Cambria County,* Tributary of Clearfield Creek, Ashville; Headwaters of Clearfield Creek, Cresson; Summit, (S. N. Rhoads coll.); Laurel Run, Lovett; *Somerset County,* Wills Creek, Mance; Flaugherty Creek and tributaries, Sandpatch; Casselman River, Rockwood; Windber; Laurel Hill, west of Jennerstown; *Indiana County,* Cush-Cushion Creek, west of Cherry Tree; Homer; Creekside; Goodville; *Jefferson County,* Mahoning Creek, Punxsutawney; Brockwayville; Brookville; *Clearfield County,* Falls Creek; *Elk County,* Elk Creek, Ridgway; *Potter County,* Keating Summit; *McKean County,* Larabee; *Warren County,* Crouse Run, Garland; *Forest County,* Tionesta; *Venango County,* Sage Run, Oil City; *Clarion County,* Alleghany River, Red Bank; *Armstrong County,* Long Run, Avonmore Station; Weskit, opposite Kittanning; Pine Creek, Mosgrove; Alleghany River, Templeton; *Westmoreland County,* Tub Mill Run, Ross Furnace, South of New Florence; Crisp (H. H. Smith and M. A. Wertheimer coll.); Lynn's Run, Mechanicsburg; Loyalhanna River, Ligonier; Indian Creek, Jones Mills; Reservoir of McGee Run, Derry; Withethorn Creek, Dundale; Livermore; Hill, opposite Leechburg; Braeburn; *Fayette County,* Youghiogheny River, Ohiopyle; Jacobs Creek, Laurelville; Dunbar; Cheat Haven; *Allegheny County,* Alleghany River, Butler Junction; Little Bull Creek, Tarentum, (A. Koenig coll.); Deer Creek, Harmarville; Little Deer Creek, Russelton; Power's Run, Montrose; Squaw Run, Aspinwall; Verona, (D. A. Atkinson coll.); Quigley's Run, Verona; Breakneck Run, Bakerstown Station; Pine Creek, below Bakerstown Station, (D. A. Atkinson coll.); Stone Run, Thornhill;

Girty's Run, Millvale; Westview (D. A. Atkinson coll.); Avalon; Edgeworth, (G. H. Clapp coll.); Schenley Park, Pittsburgh, (E. B. Williamson coll.); Fern Hollow, Pittsburgh; Edgewood Park, Swissvale; North Versailles Township, opposite Stewart; Jacks Run, South Versailles Township; Boston, (D. A. Atkinson coll.); Thompson's Run, Kennywood, (F. E. Kelly coll.); Carnegie, (D. A. Atkinson coll.); Moon Township, (D. A. Atkinson, B. Graf, E. B. Williamson, A. T. Shafer, Q. T. Shafer coll.); Thorn's Run, Moon Township; Flaugherty Run, Moon Township, (Q. T. Shafer coll.); *Butler County*, West Winfield; Renfrew; Slippery Rock Creek, Branchton; *Erie County*, Elk Creek, Girard; Walnut Creek, Swanville; *Crawford County*, Spartansburg; Linesville; *Mercer County*, Stoneboro, (D. A. Atkinson); Mercer; *Lawrence County*, Wampum; Big Run, Newcastle (D. C. Hughes coll); *Beaver County*, Ambridge; Baden; Beaver, (S. N. Rhoads coll.); Brady's Run, Fallston; Smith's Ferry; Monaca; *Washington County*, Monongahela City; West Brownsville; Francis Mine, near Burgettstown; Taylorstown; *Greene County*, Rice's Landing; Bates Fork, Deer Lick; Waynesburg; Deep Valley.

New York: *Herkimer County*, East Canada Creek, Dolgeville, (R. Ruedemann coll.).

New Jersey: *Mercer County*, Princeton.

Maryland: *Washington County*, Home's Valley, (F. Silvester coll.); *Alleghany County*, South Cumberland; Corriganville; Rawlings; *Garret County*, Selbysport; Stoyer.

West Virginia: *Morgan County*, Cherry Run; *Tucker County*, Blackwater River, Davis; Shavers Fork, Parsons; *Monongalia County*, Cheat River, (H. H. Smith coll.); Morgantown; *Pleasants County*, St. Mary's; *Wetzel County*, New Martinsville; *Marshall County*, Cameron; *Ohio County*, Elm Grove; *Brooke County*, Colliers; *Hancock County*, Holidays Cove; Congo.

Ohio: *Harrison County*, Bowerstown; *Carroll County*, New Hagerstown.

North Corolina: *Watauga County*, Blowing Rock, (Wilcox coll., Exch. Acad. Nat. Sc. Philad.).

PREVIOUS RECORDS.

Type Locality: North America, (Fabricius); Philadelphia, Pa., (Harlan).

Canada: Falls of Ouiatchouan, Lake St. John, Quebec, (Bell); Metis and Matapediac Rivers, Quebec, (Bell); Montreal, Quebec, (Faxon); Restigouche River, New Brunswick, (Bell); Upsalquitch River, New Brunswick, (Ganong); Miramichi River, New Brunswick, (Ganong); St. John, New Brunswick, (Faxon); St. John River, Grand Falls to Fredericton, New Brunswick, (Ganong).

Maine: Houlton and Maysville, Aroostock County, (Faxon); Outlet of Moosehead Lake, Piscataquis County, (Faxon); Madison, Somerset County, (Faxon).

VERMONT: (Thompson); Burlington, Colchester, and Shelburne, Chittenden County, (Faxon).

MASSACHUSETTS: (Gould); Williamstown, Berkshire County, (Faxon); North Adams, Berkshire County, (Faxon); North Crafton, Worcester County, (Faxon).

NEW YORK: Lake Champlain, (Rafinesque); Ellenburg, Clinton County, (Faxon); Elizabethtown, Essex County, (Hagen); Westport, Essex County, (Faxon); Lake George, Warren County, (Rafinesque); Saratoga County, (Rafinesque); Fishkill, Dutchess County, (Rafinesque); Newburgh, Orange County, (Rafinesque); Port Jervis, Orange County, (Faxon); New York City, (Paulmier); Fallsburg, Sullivan County, (Faxon); Fulton Lakes, Hamilton and Herkimer Counties, (Faxon); Canton, St. Lawrence County, (Faxon); Utica, Oneida County, (Rafinesque); Oswego, Oswego County, (Rafinesque); Cazenovia, Madison County, (Faxon); Sherburne, Chenango County, (Faxon); Berkshire, Tioga County, (Hagen); Ithaca, Tompkins County, (Faxon); Rochester, Monroe County, (Faxon); Niagara, Niagara County, (Hagen); Forestville, Chautauqua County, (Faxon).

NEW JERSEY: Schooley's Mountain, Morris County, (Hagen); Orange, Essex County, (Faxon); Trenton, Mercer County, (Abbott); Princeton, Mercer County (Ortmann).

PENNSYLVANIA: Windham, Bradford County, (Faxon); Headwaters of Loyalsock Creek, Sullivan County, (Ortmann); Ganoga Lake, Sullivan County, (Ortmann); Berwick, Columbia County, (Girard); Schuylkill River, Philadelphia, (Hagen); Chester County, (Faxon); Bainbridge, Lancaster County, (Faxon); Hummelstown, Dauphin County, (Faxon); Carlisle, Cumberland County, (Girard); Pinegrove, Cumberland County, (Ortmann); McKean County, (Faxon); Foxburg, Clarion County, (Girard); Westmoreland County, (Faxon); Pittsburgh, Allegheny County, (Williamson); Bedford and Loysburg,[16] Bedford County, (Faxon).

DELAWARE: Greenville, New Castle County, (Ortmann).

MARYLAND: Harford County, (Faxon); Howard County, (Faxon); Montgomery County, (Faxon); Frederick County, (Faxon); Washington County, (Faxon); Cumberland, Alleghany County, (Girard); Garrett County, (Faxon).

DISTRICT OF COLUMBIA: Georgetown, (Hagen); Washington, (Faxon).

VIRGINIA: Alexandria County, (Faxon); Clarke County, (Faxon); Stafford County, (Faxon); James River, (Faxon); Franklin, Southampton County, (Faxon); Lunenburg, Lunenburg County, (Faxon); Waynesboro, Augusta County, (Faxon);

---

[16] Faxon cites "Pattonville, Bedford County." The name of Pattonville has been changed to Loysburg, which the hamlet originally bore. It is situated in the valley known as Morrison's Cove, a beautiful spot full of clear mountain streams, formerly abounding in brook-trout. The locality must not be confounded with Pattonville in Delaware County, (P. O. Fernwood).

Rockbridge County, (Girard); Bath County, (Faxon); Pulaski, Pulaski County, (Faxon); Wytheville, Wythe County, (Faxon); Smith County, (Faxon).

NORTH CAROLINA: Kinston, Lenoir County, (Faxon); Newman's Fork, Blue Ridge, McDowell County, (Faxon); Black Mountain, McDowell County, (Faxon); Waynesville, Haywood County, (Faxon); Roan Mountain, 6,000 feet, (Faxon).

TENNESSEE: Doe River, Carter County, (Faxon); Claiborne County, (Faxon); Monroe County, (Faxon); McMinn County, (Faxon).

KENTUCKY: Kentucky River, Hickman's Landing, (Hagen)[17]; Cumberland Gap, Bell County, (Faxon); Smoky Creek, Carter County, (Faxon); Little Hickman, Jessamine County, (Faxon); Albany, Clinton County, (Faxon); Grayson Springs, Grayson County, (Faxon); Mammoth Cave, Edmonson County, (Hagen).[18]

WEST VIRGINIA: Patterson Creek, (Faxon); South Branch of Potomac River, (Faxon); Williamsport, Grant County, (Faxon); Glade Creek, Randolph County, Faxon); Petroleum, Ritchie County, (Faxon).

OHIO: Marietta, Washington County, (Faxon); Tuscarawas County, (Williamson); Knox County (Williamson); Licking County, (Williamson); Columbus, Franklin County, (Hagen); Alum Creek, and tributaries of Big Walnut and Big Darby, Franklin County, (Osborn and Williamson); Yellow Springs, Greene County, (Faxon); Warren County, (Faxon); Cincinnati, Hamilton County, (Hagen).

INDIANA[19]: New Albany, Floyd County, (Faxon); Cave near Paoli, Orange County, (Hay); Down's and Connelly's Cave, Lawrence County, (Hay); Bloomington, Monroe County, (Faxon); Clear Creek, Monroe County, (Hay); May's Cave, Monroe County, (Hay); Indianapolis, Marion County, (Faxon); Irvington, Marion County, (Hay).

The locality "Lake Superior" (Hagen) has been dropped, since it is, no doubt, erroneous, (see Ortmann, 1905, p. 135); the same is the case with "Osage River, Missouri" (Hagen).

ADDITIONAL NEW LOCALITIES.

NEW YORK: Altamont, Albany County, (N. Y. State Museum); Mill Creek, Wilmurt, Herkimer County, (N. Y. State Mus.); Spencerport, Monroe Co., (Mus. Oberlin).

PENNSYLVANIA:

Specimens preserved in the Academy of Natural Sciences of Philadelphia: 5717 Germantown Ave., Philadelphia; small stream near Holmesburg, Philadelphia County;

---

[17] Not located by writer.

[18] The form from Mammoth Cave is not typical, according to Faxon and Hay.

[19] Specimens from Indiana differ from the typical form, according to Faxon and Hay.

Roberts Run, Abrams, Montgomery County; Port Alleghany, McKean County; Corydon, Warren County.

Specimens preserved in the Department of Agriculture, Harrisburg: Buckingham, Bucks County; Avondale, Chester County; Highspire, Dauphin County; Harrisburg, Dauphin County; Rockville, Dauphin County; Dauphin, Dauphin County; Marshrun, Perry County; Gettysburg, Adams County; Montalto, Franklin County; Emmaville, Fulton County; Huntingdon, Huntingdon County; Williamsport, Lycoming County; New Albany, Bradford County; Wellsboro, Tioga County.

Mr. W. R. McConnell collected this species at the following localities: Stream flowing out of Beach Lake, Wayne County; small stream tributary to Delaware River, Portland, Northampton County; stream flowing into Lehigh River, Slatington, Lehigh County; Schuylkill River, Reading, Berks County; Toby's Creek, Kingston, Luzerne County; Fish Creek, near Stillwater "fifteen miles above Bloomsburg," Columbia County; Montour Run, Greenpark, Perry County; Big Buffalo Creek, Erly, Perry County; Conococheague Creek, Chambersburg and Marion, Franklin County; tributary of Conococheague Creek, Mercersburg, Franklin County; Laurel Run and Shafer's Run (probably Shaver's Creek, both in northeastern part of county), Huntingdon County; Slab Cabin Creek and Thompson's Spring, State College, Center County; Bear Meadows and branch of Spring Creek, Boalsburg, Center County; Sinking Creek, Center Hall, Center County; Bald Eagle Creek and Wallis Run, Milesburg, Center County; Beech Creek, Beech Creek Station, Clinton County; Fishing Creek and tributary, Lamar, Clinton County; Nipponose Creek, Jersey Shore, Lycoming County; branch of Genessee River, Ulysses, Potter County.

The writer has seen this species at and from the following localities:

Lafayette, Montgomery County, (H. Gera coll.); Leopard, Easttown Township, Chester County, (J. F. Sachse, Philadelphia, coll.); Wills Creek, Hyndman, Bedford County; Big Meadow Run, Ohiopyle, Fayette County; West Branch of Susquehanna, Cherry Tree, Cambria and Clearfield Counties.; Blairsville Intersection, Westmoreland County; Springs on Chestnut Ridge, near Derry, Westmoreland County, elevation 1800 feet; Coalpit Run, Millbank, Westmoreland County; Donegal, Westmoreland County; Jeanette, Westmoreland County; Alleghany River, Hulton, Allegheny County; tributary of Thompson's Run, south of North Bessemer, Allegheny County; Sandy Creek and Alleghany River, Sandy Creek, Allegheny County; Nine Mile Run, Pittsburgh, Allegheny County; Dinsmore, Washington County; Summit and Conneautville Station, Crawford County.

MARYLAND: Sideling Creek, Washington County, (H. A. Pilsbry coll., Acad.

Nat. Sc. Phil.); Town Creek, Alleghany County, (H. A. Pilsbry coll., Acad. Nat. Sc. Phil.); Deer Park, Garrett County, (P. R. Uhler coll.). (See below under *C. diogenes*, footnote 26.)

REMARKS:

Cambarus bartoni is the crawfish of the small streams in Pennsylvania, and is exceedingly abundant all over the state.

In spite of its wide distribution over parts considerably different in physical conditions, this species is in Pennsylvania very uniform with regard to its morphological characters (disregarding the variety *robustus*, to be discussed below). It is true that in the foregoing description many characters are pointed out which vary within certain limits; but these variations are not restricted to certain parts of the state, but occur everywhere. It is even hard to say of any character that it prevails in a certain region. In general there are indications that the species is more flourishing and also more variable in the western part of the state than in the eastern. This observation, however, applies chiefly to characters which appear in very old specimens, as for instance, a stronger development of the tubercles on the inner margin of the hand and on the outer margin of the movable finger. Since the eastern form is much smaller, such characters, which are only occasionally present in very large specimens, are not found in specimens from the east, namely, strong sculpture of the hand and very thick margins on the rostrum.

The most variable feature of this species is the rostrum. Generally it is narrower and more gradually tapering in very young specimens (Pl. XXXIX, Fig. 1*d* and 1*e*). In older individuals it becomes broader, and is more suddenly constricted into a longer or shorter acumen. Beyond this there is no rule. The most frequent shapes are those figured on Pl. XXXIX, Fig. 1*b* and 1*c*. The one delineated in Fig. 1*f* is exceptional. The other extreme is shown in Fig. 1*a*, with margins practically parallel, and a very sudden constriction into a comparatively short and broad acumen. Although this last shape is more frequent in the western part of the state, it is also found in the extreme eastern portions of the commonwealth.

There is only one character in which regional variation may be observed, and this is the size of the body. As has been mentioned, in the eastern part of the state this species is considerably smaller than in the western, and the largest specimens are found west of the Chestnut Ridge. Individuals 80 mm. and more in length are not rare in Westmoreland, Allegheny, Elk, and Lawrence Counties. Specimens between 70 and 80 mm. long have been found, in addition to the counties just named, in Crawford, Venango, Potter, Jefferson, Butler, Armstrong, Washington, and

Fayette. All of these are west of the Chestnut Ridge. East of the Chestnut Ridge, but west of the Alleghany Front, specimens over 80 mm. in length are rare; only one was found at Sand Patch, Somerset County, (86 mm. long). Specimens over 70 mm. in length are not infrequent here. In the Alleghany Mountain region, (between the Alleghany Front and the Blue Ridge) only a few instances of specimens over 70 mm. in length have been found, and none as large as 80 mm. The largest is from McConnelsburg, Fulton County, 77 mm. East of the Blue Ridge (South Mountain) the length 70 mm. is never attained. In the easternmost extremity of the state (Northampton and Bucks Counties) even the length of 60 mm. is not represented among my material, although I possess large series of specimens from this region. Thus it appears that the size gradually decreases from west to east. There is hardly any appreciable decrease in size from south to north. The smaller number of large individuals from the northwestern section of the state is very likely due to the fact that large collections were not made in that part of the state.

Freaks have been observed in several cases. Aberrant forms of the rostrum have been repeatedly found, and one variation has been encountered four times in which the rostrum has a very slightly developed acumen, so that it is almost evenly rounded off anteriorly, with only a small and indistinct median angle or point, (female, 25 mm., Schenley Park, Pittsburgh; female, 50 mm., Templeton, Armstrong County; male, first form, 64 mm., Branchton, Butler County; female, 80 mm., Monongahela City, Washington County). The rostrum, in these cases, is exceptionally short, due to a reduction of the acumen. A case of an unsymmetrical rostrum, with the left angle at the base of the acumen cut off, has also been observed; this is clearly a malformation due to some previous external injury.

We may class with the freaks a single specimen in which the carapace possesses a lateral spine. The specimen is a female (42 mm. long) from Weskit, Armstrong County, and it has a small, sharp, lateral spine, but only on the left side of the carapace. This is the more remarkable since it demonstrates the importance of this specific character. There is not a single other individual among the large material at hand which possesses such a spine, although granulations in its place are not infrequent.

Two interesting cases of abnormally developed sexual characteristics have been noticed (compare the other cases mentioned under *C.* (*Faxonius*) *obscurus*).

1. A large female, 71 mm. long, found March 31, 1905, at Hollidays Cove, Hancock County, W. Va., (Cat. No. 74. 491), which is normal in every respect but one, and besides, is undoubtedly sexually normal, since it carried under the abdomen

ten young ones, ready to leave the mother, (very likely a number had left already when the mother was captured). It has on the ischiopodite of the left third pereiopod the copulatory hook of the male; this hook is not small or rudimentary, but strong, and similar to the hook as found in the male of the first form. The ischiopodite of the corresponding right pereiopod has no trace of this hook.

2. A specimen, 48 mm. long, was found in Fern Hollow, Pittsburgh, November, 22, 1905, (Cat. No. 74. 681), which externally (in the shape of the claws) looks like a female, but shows very indistinctly the sexual openings of the male, and no traces of those of the female. It also has the first pleopods of the male of the second form, but the second pleopods are built according to the female type. Further, it lacks entirely the hooks of the third pereiopods, and has a distinct female annulus, of juvenile type.

This case does not correspond exactly to any of those described previously. It resembles to a certain degree one of the cases in *C. obscurus* described above (No. 3), with the exception that here the first pleopods are of the type of the male of the second form, and that the second pleopods are not of the male, but of the female type.

4*a*. CAMBARUS (BARTONIUS) BARTONI ROBUSTUS (Girard).

(Plate B, Fig. 2. Plate XXXIX, Fig. 2*a* and 2*b*. Plate XL, Fig. 3.)

Cambarus robustus Girard, 1852, p. 90; Hagen, 1870, p. 80, Pl. 3, f. 167; Smith 1874, p. 639; Faxon, 1884*b*, p. 143.

Cambarus bartoni robustus Faxon 1885*a*, p. 61; Faxon, 1885*b*, p. 358; Underwood, 1886, p. 367; Faxon, 1890, p. 622; Faxon, 1898, p. 649; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20. 47; Hay, 1899, p. 959, 966; Williamson, 1901, p. 11; Ortmann, 1905*a*, p. 391; Ortmann, 1905*b*, p. 135.

Cambarus bartoni Williamson, 1905, p. 310.

The differential characters of this form are the following:

Body robust, attaining decidedly a more considerable *size* than the typical *bartoni*. The largest individuals at hand are a male, first form, from Spartansburg, Crawford County, measuring about 98 mm. (estimated, since rostrum is damaged); a female from Squaw Run, Allegheny County, measuring 94 mm. and a male, second form, from Puketta Creek, Allegheny County (A. Kœnig coll.), measuring 101 mm. I have quite a number of males (of the first and second form) and of females over 90 mm. long. It is also remarkable that specimens of this variety, of a considerable size (60 to 70 mm.) display characters which are distinctly juvenile, showing no tendency on the part of the chelæ to attain a large size. This tendency is also evidenced by the fact that the smallest males of the first form at hand are two individuals measuring 72 mm. (Union City and Hulton). From Oberlin, Ohio, I have seen a male of the first form, 71 mm. long, while the minimum size of sexually ripe males of the typical form is 50 mm. for western, and 49 mm. for eastern Pennsylvania.

The shape of the carapace is similar to that of *C. bartoni*, but, in old specimens, appears slightly more depressed on account of the wider hepatic and branchial regions; G : H : B = 1 : 1.3 to 1.5 : 1.5 to 1.7.

The *rostrum* (Plate XXXIX, Figs. 2*a* and 2*b*) is markedly different from the typical form, narrower, more tapering, and with a longer acumen; the upper surface is slightly concave. The shape is rather variable. In young specimens of the typical *C. bartoni* the rostrum often approaches the form of *C. bartoni robustus*, but on the other hand young specimens of the latter have a narrower rostrum than the former. (Compare Plate XXXIX, Fig. 1*e* and 2*b*). In many cases the rostrum of the variety is not longer than in the typical form, but in others it surpasses it, reaching to the middle, or even almost to the end of the third joint of the peduncle of the antennula, or to the base or almost to the middle of the fifth joint of the peduncle of the antenna.

Areola similar to that of the typical form, but with a larger number of rows of punctures (4–6), which is due to the punctures being more crowded, not only on the areola, but on the whole carapace.

The *carapace* is often provided with small and sharp *lateral spines;* they are sometimes obsolete, or replaced by tubercles, or even entirely absent.

Antennal scale generally slightly wider than in the typical form, and slightly longer.

Antennal flagellum not differing greatly from that of the typical form, and quite variable in length. There are a few cases where it reaches to the end of the telson, and even slightly beyond, thus surpassing any case known in *C. bartoni*.

The *first pereiopods* (Plate XL, Fig. 3), display remarkable and important differences from the typical form. The hand has nearly the same shape, but the fingers are less gaping, and meet all along their edges even in individuals of a considerable size (retention of juvenile character); it is only in very large specimens that they are distinctly gaping, but less so than in much smaller individuals of *C. bartoni*. The sculpture of the hand is much more strongly developed. The inner margin of the hand has a distinct and regular *double* row of tubercles. This double row is a very important character, and is noticeable in specimens from the size of about 30 mm. upward. In very young individuals it is obsolete, and becomes more and more distinct with advancing age. Every specimen at hand, without exception, possesses this character, when the chelæ are normally developed; but it must be mentioned that in regenerated chelæ, which are always recognizable by their shape, this double row is sometimes indistinct or irregular. Further, there is a triangular depression both on the upper and lower side of the hand at the base of the immovable finger. Both impressions are always present in large individuals; in younger ones they are indistinct, but are always marked by punctures, which are much crowded, and consequently by the denser hairs implanted in them. Traces of the impression on the upper surface are often seen in the typical form, but that of the lower surface is always absent, or marked only by a slight flattening of the surface. These two impressions give to the hand of this variety a very strongly marked marginal keel or ridge. The outer margin of the movable finger possesses a number of irregularly placed tubercles, indistinct, and restricted to the proximal part in young specimens, but very distinct, and occupying about two-thirds or three-fourths of the margin in old specimens. The longitudinal ribs of the upper surface of the fingers are always well developed, and there is hardly any tendency in older specimens for them to become obscure, chiefly in the case of the immovable finger, where this rib is always well marked on account of the strongly developed punctures of the depression accompanying it on the outside.

The armature of the *carpopodite* and the *meropodite* is almost identical with that of the typical form, but the carpopodite in old individuals is often provided with accessory low tubercles on the upper face. The spines of the meropodite are more distinct and more numerous; those on the distal upper margin (generally two of them) well developed, even in large individuals; those of the lower margin consisting of two to six in the outer row (two are rare, found only in young ones; in regenerated chelæ as many as eight); and seven to twelve in the inner row (as many as fourteen in regenerated chelæ).

All the other characters, including the *color* (see Plate B, Fig. 2), agree with the typical form. The color of the eggs (in the only specimen ever found with eggs, at Spartansburg) is prune-purple (VIII, 1), almost black.

There are in the collections of the Carnegie Museum one hundred and forty-seven specimens of this form, all of which are from Pennsylvania, with the exception of four, which are from Kentucky.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

Pennsylvania: *Allegheny County*, Chartiers Creek, Carnegie, (D. A. Atkinson coll.); Pine Creek, below Bakerstown Station, (D. A. Atkinson coll.); Squaw Run, near Aspinwall; Alleghany River, Sandy Creek; Alleghany River, Hulton; Little Bull Creek, Tarentum, (A. Koenig coll.); Puketta Creek, (A. Koenig coll.); *McKeen County*, Alleghany River, Larabee; *Warren County*, Crouse Run, Garland; *Crawford County*, Oil Creek and tributaries, Spartansburg; small tributary of Conneaut

Creek, Conneautville Station; *Erie County*, French Creek, Union City; Sixteen Mile Creek, Northeast, (Miss G. Kinzer coll.); Walnut Creek, Swanville; Elk Creek, Girard; Conneaut and Temple Creeks, Albion.

KENTUCKY: Small stream tributary to Rockcastle River, Livingston, Rockcastle County, (E. B. Williamson coll.).

PREVIOUS RECORDS.

Type locality: Humber River, Toronto, Ontario, Canada, (Girard).

CANADA: Don River, Toronto, Ontario, (Faxon); Weston, Ontario, (Faxon).

NEW YORK: Tributary of Racket River, near Tupper's Lake, St. Lawrence County, (Faxon); Canton, St. Lawrence County, (Faxon); Natural Bridge, Jefferson County, (Faxon); Fulton Lakes, Hamilton and Herkimer Counties, (Faxon); Petersboro, Madison County, (Faxon); Sodus, Wayne County, (Faxon); Genessee River, Rochester, Monroe County, (Hagen); Forestville, Chautauqua County, (Faxon).[20]

PENNSYLVANIA: Squaw Run, near Aspinwall, Allegheny County, (Williamson); tributary of Alleghany River, Port Alleghany, McKean County, (Ortmann).

OHIO: Big Jelloway Creek and tributaries, Knox County, (Osburn and Williamson); Oberlin, Lorain County, (Ortmann).

ILLINOIS: Decatur, Macon County, (Faxon).[21]

MARYLAND: Montgomery County, (Faxon).

VIRGINIA: Fredericksburg, Spottsylvania County, (Hagen); Wytheville, Wythe County, (Faxon).

New Localities:

PENNSYLVANIA: Waterford, Erie County, (Dep. Agriculture, Harrisburg).

MARYLAND: Deer Park, Garrett County, (P. R. Uhler coll., see below under *C. diogenes.* Footnote 27).[22]

REMARKS:

In Pennsylvania this variety is well marked, and might safely be regarded as a species. Its chief characters are found in the shape of the rostrum and the sculpture of the hand. I never was in doubt as to this form, with the exception of young individuals (less than 30 mm. long), in which the hand does not show its characteristic features; but in such specimens the shape of the rostrum generally gives a clue. This, however, is not the case in *very* young specimens, (less than 20 mm. long), and such I am unable to distinguish from the typical form.

---

[20] Hagen also gives: "Regis Lake, N. Y.", in the Adirondacks.

[21] This locality should be confirmed, see Ortmann, 1905*b*, p. 135.

[22] In Rough Run, West Winfield, Butler County, Pa., I found on June 20, 1904, several young specimens apparently belonging to this variety. I did not take them, expecting to get larger ones, in which hope I was disappointed. Thus this locality is somewhat doubtful.

The characters are slightly variable, as has been pointed out above, but this variety generally is very uniform in its characters in Pennsylvania. I have not found any variations worthy of special mention. With reference to the lateral spine of the carapace, there are specimens which show no trace of it, (young as well as old). In old specimens this spine is often tuberculiform, and in about half of the number at hand there is on each side a sharp, but always small lateral spine. In this respect there is no difference in the specimens of northwestern Pennsylvania from those found in Allegheny County.

It seems to me that the southern records for this variety (Maryland, Virginia, and also Kentucky)[23], do not refer to exactly the same form which is found in the north (Canada, New York, northwestern Pennsylvania, northern Ohio). Hay (1899, p. 966), in the key to the species gives as one of the differential characters of *C. bartoni robustus*: "carapace cylindrical, sides nearly parallel as far forward as cervical groove, then curving abruptly to the base of rostrum," while, under *C. bartoni*, the carapace is described as " . . . depressed, sides gently curving toward the front and rear." This cylindrical shape of the carapace is decidedly *not* present in our northern form; on the contrary, the depression of the carapace in our *robustus* is, if anything, more pronounced than in the typical *bartoni*; and our *robustus* agrees in this respect with Girard's type from Canada, preserved in the Academy of Natural Sciences, Philadelphia, and which has been examined by the writer.

On the other hand, our specimens from Kentucky seem to approach the form from Virginia and Maryland. The shape of the carapace is more cylindrical, as Hay describes it, $G:H:B = 1:1.05$ to $1.2:1.2$ to 1.3. This shows that the width of the carapace at the branchial and hepatic regions is decidedly less, compared with the vertical diameter at the gastric region, than in the typical *bartoni*. There are other slight differences in the form from Kentucky: (1) the rostrum is not quite so narrow; (2) the lateral spine of the carapace is absent; (3) the punctures of the areola are not so crowded (about three rows), and are similar to those of *bartoni*; (4) the impressions of the hand are indistinct; (5) the double row of tubercles on the inner margin of the hand is different, the outer row being distinct, but the inner consisting of only a few more or less distinct irregular tubercles. All four specimens from Kentucky are comparatively small, (the largest is 54 mm. long), and thus the two last described characters may be due to age, although the specimens differ slightly from northern individuals of the same size. The other characters incline toward the typical *bartoni*, while the shape of the carapace varies to the other extreme.

---

[23] Faxon, 1890; Hay, 1899; Williamson, 1905; Ortmann, 1905*b*.

A single male of the second form, about 60 mm. long, from Deer Park, Garrett County, Maryland, sent to me for examination by Dr. P. R. Uhler of Baltimore, was found under a lot of typical *C. bartoni*, (supposed to be *C. diogenes*). This male agrees fairly well with the specimens from Kentucky. The carapace is rather cylindrical; there are no lateral spines on the carapace; the punctures of the areola are like those of *C. bartoni;* the chelæ, which are unequal, and apparently both regenerated, have rather distinct impressions on the upper surface, but the inner margin has only one row of tubercles. The rostrum is of the *robustus*-type. Thus, of the characters of *robustus*, only the shape of rostrum and the impressions of the chelæ were present, all other characters being those of typical *bartoni*.

Specimens possessing a rather elongated rostrum, but with the other characters of typical *bartoni*, I have seen associated with individuals of the typical form taken at Gettysburg, Adams Co., Pa. (Dep. Agric., Harrisburg); but these I have recorded with typical *C. bartoni*. (See above, p. 385.)

It is very desirable that the southern form in Maryland, Virginia, Kentucky, and adjacent localities, should be investigated more closely. The records at hand, and the few, immature specimens the writer has seen, do not permit a final conclusion as to whether we have to deal in the south with a form differing from that in the north, or not. The same reason forbids us to restore our *C. robustus* to the rank of a species, which I surely would have done if the Pennsylvanian material alone were to be considered.

In Pennsylvania *C. bartoni robustus* is not always associated with *C. bartoni*. I found it thus in every case in Allegheny County, in Crawford County, and in Warren County. In McKean County I found it associated with *C. obscurus* in the Alleghany River at Larabee, but the typical *C. bartoni* was not there, although occurring not far away in small streams and springs. In Erie County *C. bartoni* was found only twice, in Elk Creek and Walnut Creek, associated with *C. bartoni robustus*, but then only a single individual of the former was found in each case. At Albion and Union City *C. bartoni robustus* alone was present, and I am sure of it, since I hunted for *C. bartoni*, but without success. The rich material from Northeast (forty-four specimens are now in the Museum, but many more were originally in the lot) did not contain a single *C. bartoni*. Thus it is beyond doubt that *C. bartoni robustus* is not infrequently found *without* the typical form, and chiefly so in the most northern and western sections of the state.

5. Cambarus (Bartonius) carolinus Erichson.

(Plate A, Fig. 4; Plate XXXIX, Fig. 3*a* and 3*b*, and 9; Plate XL, Fig. 4).

Astacus (*Cambarus*) *carolinus* Erichson, 1846, p. 96.

Cambarus dubius Faxon, 1884*b*, p. 114; Faxon, 1885*a*, p. 70, Pl. 4, f. 3, Pl. 8, f. 7; Underwood, 1886, p. 368; Faxon, 1890, p. 624; Hay, 1899, p. 959, 965.

Cambarus carolinus Hay, 1902*b*, p. 38; Ortmann, 1905*a*, p. 393.

Cambarus (*Bartonius*) *carolinus* Ortmann, 1905*b*, p 120, 135.

Body robust, smooth, except for short hairs, chiefly on the chelæ in freshly moulted individuals.

Carapace subovate, not depressed, but rather compressed in comparison with the species described above. $G:H:B = 1:1.07$ to $1.1:1.1$, that is to say, the vertical diameter and the transverse diameters of the hepatic and branchial regions are practically the same, the two transverse diameters being only slightly greater than the vertical. The greatest width of the branchial regions is well forward, immediately behind the cervical groove.

Cervical groove deep, not interrupted on the sides.

Areola distinctly longer than half of the anterior section of the carapace ($a:p = 1:1.65$ to 1.74), very narrow ($w:l = 1:10$ to 15), with only one, or rarely two, very irregular rows of punctures, which occasionally are almost entirely lacking.

Rostrum (Pl. XXXIX, Fig. 3*a* and 3*b*) slightly curved downward toward the tip, broad and short, never reaching beyond the distal end of the second joint of the peduncle of the antennula, but generally only to the middle of it, being sometimes even shorter than that. Upper surface slightly concave, with elevated margins. Margins straight, sub-parallel, or slightly converging toward the tip, suddenly contracted into a broad, short, triangular acumen. Basal angles of acumen rather sharp, but without any trace of marginal spines. These angles are emphasized by the sudden disappearance of the slight swelling of the lateral margins, which are not at all swollen on the acumen. Acumen pointed, but point short. Postorbital ridges short, almost parallel, ending bluntly anteriorly.

Surface of carapace punctate, granulated only on the hepatic region, and sometimes with a few indistinct granules immediately behind the cervical groove on the branchial region. No lateral spine. External orbital angle rarely or not at all marked, generally formed by a rounded or slightly angular, insignificant projection, but never with a spine. Branchiostegal spine formed by a small, often indistinct, tubercle.

Abdomen always distinctly shorter than the carapace, narrower than the latter in the male, almost as wide as the carapace in the female. Anterior section of *telson* on the posterior lateral corners with one or two spines. Posterior section semi-elliptical, distinctly wider than long, about as long as the anterior section.

Epistoma with posterior part comparatively long, hardly one and one-half times as broad as long; transverse groove indistinct and close to posterior margin; anterior median depression also indistinct, and thus the posterior part of the epistoma appears rather flat and smooth. Anterior section constricted at base, semi-circular or semi-elliptical or subquadrate, rarely with a median anterior point, often more or less truncate anteriorly, or even slightly emarginate. Transverse diameter never greater than longitudinal, as great as the latter or shorter.

Antennula with a small tubercle on the lower margin of the basal joint.

Antennal peduncle without distinct spines or tubercles on the two proximal, joints.

Antennal scale short and small, slightly longer than the rostrum, and not reaching beyond the distal end of the fourth joint of the antennal peduncle. Spine of outer margin strong. Laminar part only slightly wider than the spine.

Flagellum short, not reaching beyond the third abdominal segment in the male, and not beyond the second segment in the female, but often hardly longer than the carapace.

First pereiopods (Pl. XL, Fig. 4) short, not very robust, not undergoing much change with age, and not differing much according to sex. Hand ovate, broad and depressed. Surface punctate. Inner margin of palm convex, with a single row of distinct tubercles, larger proximally; occasionally there is a second, incomplete row inside of and parallel to this. Outer margin smooth and rounded proximally for a short distance, but soon becoming angular and forming a distinct ridge along the edge in the region of the base of the immovable finger. This ridge has a regular row of deep punctures, giving the distinct appearance of serrations along the outer margin of the hand. Fingers as long as, or slightly longer than the palm, slightly gaping at the base in both young and old individuals, straight. Outer margin of movable finger with punctures, but very rarely with tubercles. Cutting edges with a few irregular tubercles in the proximal half. Upper surface of each finger with a low rib, bordered by rows of punctures.

Carpopodite slightly longer than wide, about as long as the palm, with a deep longitudinal sulcus above. There is always a strong, more or less pointed, spine on the inner margin, directed obliquely forward, and a strong, often spiniform, conical tubercle in the middle of the anterior margin of the under side, (rarely obsolete). The tubercle at the lower articulation with the hand is low and indistinct. Rarely there are accessory tubercles, which, however, are never spiniform. The most frequent are a proximal tubercle on the inner margin, and one between the two larger spines first mentioned, and another just behind the base of the large spine of the inner margin.

Meropodite smooth, with 1–3 indistinct tubercles near the distal end of the upper margin, often entirely obsolete. Lower side with two rows of spiniform tubercles. The outer row consists of 2–6 (if only 2, they are followed by a few undulations produced by punctures); the inner consists of 6–11 tubercles. Outer articular tubercle with carpopodite without spine. All spines of the first pereiopods are indistinct in very young specimens.

Ischiopodite of third pereiopod hooked in the male. Hook of the male of the first form strong, subconical.

Coxopodite of fourth pereiopod in the male with a prominent, blunt, and slightly compressed subconical tubercle.

First *pleopods* of the male (Plate XXXIX, Fig. 9) similar to those of *C. bartoni.*

Annulus ventralis of the female likewise of the type of *C. bartoni,* but less transverse, and the posterior margin more swollen and elevated, while the anterior is hardly elevated at all, but depressed.

Size. — The largest male of the first form at hand is from Dunbar, Fayette County, and measures 67 mm. in length. The largest female is from Ohiopyle, Fayette County, and measures 80 mm. in length.

Color (Plate A, Fig. 4). — Whole body rather uniformly *orange-chrome* (Ridgway, 1886, VII, 13) to *chinese-orange* (VII, 15), very brilliant in fresh shells, shading to *orange-rufous* (VII, 12) and *cream-color* (VI, 20) on the sides. Color most intense on anterior part of carapace and on the claws. Abdomen *orange-chrome,* shading to *salmon-color* (VII, 17) or *ferrugineous* (IV, 10), or *ochraceous-buff* (V, 13). Chelæ varying from *orange-chrome* to *saturn-red* (VII, 16). Legs *chinese-orange* to *salmon-color* and *ferrugineous.* Often a brown or blackish coat of mud covers a great part of the body, obscuring the colors. The color of young specimens is semitransparent, with more or less red prevailing, but the rostrum and chelæ are always distinctly red. Color of eggs *salmon* (VII, 17) to *salmon-buff* (IV, 19).

There are one hundred and thirty-eight specimens in the Carnegie Museum; ninety-three from Pennsylvania, thirty-six from West Virginia, and nine from Maryland.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: *Westmoreland County,* Jones Mills; *Fayette County,* Dunbar; Indian Creek; Rainier Park, Ohiopyle; *Somerset County,* Windber; Listie; Rockwood; Myersdale.

MARYLAND: *Garrett County*, Selbysport.

WEST VIRGINIA: *Preston County*, Reedsville; *Tucker County*, Parsons; *Mineral County*, Schell.

PREVIOUS RECORDS.

Type locality: Greenville, Greenville County, S. C., (Erichson and Faxon, 1885*a*, pp. 9, 56).

TENNESSEE: Cumberland Gap, Claiborne County, (Faxon).

VIRGINIA: Pennington Gap, Lee County, (Faxon).

WEST VIRGINIA: Southwestern West Virginia, (Hay); Terra Alta (Cranberry Summit), Preston County, (Faxon).

INDIAN TERRITORY: Cherokee Nation, (Faxon).[24]

New Locality:[25] Blowing Rock, Watauga County, North Carolina, (J. P. Moore coll., Acad. Nat. Sci. Philadelphia).[26]

REMARKS:

This species, the Red Crawfish of the mountain regions, occupies, next to *C. propinquus*, the smallest area in this state. Its morphological characters are very uniform, not only in this state, but also in the neighboring parts of West Virginia and Maryland. The chief variations, as already mentioned in the description, are found in the armature of the chelipeds, but they keep within comparatively narrow limits. The rostrum, which is quite variable in *C. bartoni*, is here very constant, only the degree of convergence of the lateral margins and the length of the acumen varying to a certain extent, (See Pl. XXXIX, fig. 3*a* and 3*b*.) Of course, we must disregard monstrosities, under which head I place two cases, (from Dunbar and Parsons), where the rostrum has almost no acumen at all, being rounded off apically.

The armature of the meropodite and carpopodite varies as described above; the carpopodite in particular showing a various number of tubercles, though they never become spiniform as in *C. monongalensis*. The lower outer margin of the meropodite has always more than one spine, when spines at all are visible, which is generally not the case in very young individuals.

---

[24] This locality needs confirmation, see Ortmann, 1905b, p. 135.

[25] This species is abundant in certain parts of Somerset and Fayette Counties, Pa., and well known to the natives. I have seen chimneys in abundance at Confluence, Somerset County, which undoubtedly belong to this species, but was not able to secure specimens, my time being limited. I have seen a specimen at Flanigan, 4 miles north of Somerfield, Fayette Co., and one from Humbertston, Fayette Co. (O. T. Cruikshank coll.). Reports received from farmers, always emphasizing the red color and burrowing habits of the crawfish in question, are the following: Great Meadow Run, west of Ohiopyle, Fayette County; Millrun, Fayette County; Ursina, Somerset County; Salisbury, Somerset County.

[26] These specimens (collected June, 1893, and, according to Professor Moore's recollection, dug out of holes) agree in all essential points with our material, only the rostrum is narrower.

I think I have observed that in specimens from the south (Maryland and West Virginia) there is a more pronounced tendency to develop a second row of tubercles at the inner margin of the hand. Such specimens, with a few additional tubercles, occur also in Pennsylvania, but in West Virginia they are more frequent, and the additional row becomes more distinct and more regular. There is moreover a specimen from Parsons, W. Va., in which traces of a third distal row are visible. On the other hand specimens with one row only are also found in West Virginia.

No interesting freaks or monstrosities have been observed.

6. CAMBARUS (BARTONIUS) MONONGALENSIS Ortmann.

(Plate B, Fig. 4. Plate XXXIX, Fig 4*a*, 4*b* and 10. Plate XL, Fig. 5.)

Cambarus dubius Williamson, 1901, p. 11, (non *dubius* Faxon).
Cambarus monongalensis Ortmann, 1905*a*, p. 395.
Cambarus (*Bartonius*) *monongalensis* Ortmann, 1905*b*, p. 120.

This species being closely allied to *C. carolinus*, the description will be given in terms of comparison with the latter.

General shape of *body*, *carapace*, *cervical groove*, and *areola* identical with that in *C. carolinus*. $G : H : B = 1 : 0.9$ to $1.1 : 1.1$ to 1.3.

Rostrum (Pl. XXXIX, Figs. 4*a* and 4*b*) markedly different from that of *C. carolinus*. It is as long as that of the latter species, or slightly shorter in the average, never reaching beyond the middle of the second joint of the antennula, and is uniformly narrower. The upper surface is concave. The margins are less sharply elevated, the elevation decreasing gradually to the apex. Margins distinctly converging, and contracted to form the short, triangular acumen, but the contraction is not so sudden as in *C. carolinus*, so that the angles at the base of the acumen are not so sharp, but rounded. Acumen with short point. Postorbital ridges short and rather indistinct, distinctly divergent posteriorly.

Sculpture of carapace and other details as in *C. carolinus*. The *abdomen* and *telson* are also identical, but the lateral corners of the anterior section of the telson have only one spine.

Epistoma similar to that of *C. carolinus*, but the truncated (subquadrate) shape prevails in the anterior section, which has often a small median anterior point.

Antenna and *antennula* similar to those of *C. carolinus*, but *antennal scale* shorter, not much longer than the rostrum, and reaching only to the middle of the fourth joint of the antennal peduncle.

First pereiopods (Pl. XL, Fig. 5) in general shape similar to those of *C. carolinus*, but hand not quite so broad, and there are important differences in the armature. The inner margin of the hand invariably has only one, but a distinct, row of tubercles. The outer margin is rounded, with no indication of angulation, and entirely lacks the serrations of *C. carolinus,* the punctures producing the latter forming in this species no regular row.

The *carpopodite* is much more spinous. The large spine of the inner margin is well developed. The spine in the middle of the anterior margin of the under side is tuberculiform, and the tubercle at the lower articulation with the hand is insignificant. But there always are additional distinct spines, which are well developed, although smaller than the large spine of the inner margin. A spine on the proximal end of the inner margin is always present, and also a spine between the large spine of the inner margin and the anterior tubercle of the lower side. (If the latter spine is missing, the claw has been regenerated.) Often there are other spines. The proximal spine of the inner margin may be double, and there may be one or several spines or tubercles near the base of the large spine of the inner margin, anterior or posterior to it.

Meropodite with the distal tubercles of the upper margin very indistinct, generally missing. The outer lower margin is formed by a smooth keel, which has in most cases only one small tubercle near the distal end, which may be obsolete. In rare instances there are two tubercles. If there are more, the claw has been regenerated. The inner lower margin has a row of 6–12 spiniform tubercles; if less, the claw has been regenerated.

All the other organs are similar to those of *C. carolinus,* more particularly the first pleopods of the male (Pl. XXXIX, fig. 10) and the annulus of the female.

Size. — The largest male of the first form, from Edgewood Park, Allegheny County, is 68 mm. long; the largest females (same locality and Monaca, Beaver County), are 76 mm. long.

Color (Pl. B, Fig. 4). — In specimens with fresh shells the middle of the carapace and abdomen is of a beautiful *marine-blue* (Ridgway, 1886, IX, 2); the hepatic and branchial regions are *cyanine-blue* (IX, 3) and *china-blue* (IX, 13), shading toward the lower margin to *pale-blue* (IX, 16). The marine-blue of the abdomen is restricted to the anterior parts of the segments; the posterior parts and the epimera are *china-blue* shading to *pale-blue.* Margins of rostrum *maroon-purple* (VIII, 9). The hand is *cyanine-blue* above, shading toward the lower side to *cobalt-blue* (IX, 12), *azure-blue* (IX, 15) and *pale-blue.* At the base of the dactylopodite there is a good deal of *royal-purple* (VIII, 7). The dactylopodite is *cyanine-blue,* the outer margin *violet* (VIII, 10). The finger-tips are *orange-vermilion* (VII, 12), shading proximally to *salmon-color* (VII, 17) and whitish. The carpododite of the chelipeds is *marine-blue,* shading to *cyanine-blue* and *French-blue* (IX, 6). Tubercles and spines of hand and carpopodite pale *vinaceous-pink* (lighter than IV, 21). Basal joints of antennæ *cyanine-blue;* flagellum annulated *dahlia-purple* (VIII, 2) and very pale *lilac* (lighter than VIII, 19). Pereiopods *pale-blue,* upper edges shading to *china-blue,* near the bases *white.* Lower side of body whitish, on the abdomen suffused with *china-blue* and *pale-blue.*

These brilliant colors fade more or less in old specimens, but the *marine-blue* always remains the ground-color. A brownish or blackish deposit of mud often obscures the colors, and such specimens often appear *blackish-blue* all over.

Young individuals are semitransparent, with a distinct *pale-blue* hue on the abdomen and chelæ, and *heliotrope-purple* (VIII, 18) on the carapace.

Distinct color varieties are rare, and the few observed will be mentioned below.

The color of the newly laid eggs is *hazel* (IV, 12) or *ochraceous* (V, 7); later on they are *vinaceous-buff* (V, 15) on one side, *pinkish-white* on the other.

The Carnegie Museum possesses two hundred and seventy-nine specimens of this species, two hundred and thirty-six of which are from Pennsylvania, and forty-three from West Virginia.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

Pennsylvania: *Westmoreland County,* Hill, (opposite Leechburg); Braeburn; Dundale; Jeanette; *Allegheny County,* south of Logan's Ferry, (C. V. Hartman coll.); Hulton, (R. Dornberger coll.); Wilkinsburg, (D. A. Atkinson coll.); Edgewood Park, (type locality); Nine-Mile Run, Pittsburgh; Fern-Hollow, Pittsburgh; Schenley Park, Pittsburgh; Squaw-Run, near Aspinwall, (D. A. Atkinson); North Versailles Township, (opposite Stewart); Jack's Run and Long Run, South Versailles Township; Boston, (D. A. Atkinson); Thompson's Run, Kennywood, (F. E. Kelley coll.); Carnegie, (D. A. Atkinson); Moon Township, (A. T. Shafer coll.); Lashell's Hollow, Moon Township: *Beaver County,* Doctor Heights, Monaca; *Washington County,* Francis Mine near Burgettstown; Taylorstown; Monongahela City; West Brownsville; *Fayette County,* Smithfield; Cheat Haven; *Greene County,* Deer Lick.

West Virginia: *Hancock County,* Congo; Hollidays Cove; *Brooke County,* Colliers; *Ohio County,* Elm Grove; *Marshall County,* Cameron; Nuss; *Monongalia County,* Morgantown.

PREVIOUS RECORDS.

The only previous records are those given by Williamson (as *C. dubius*), Schenley Park and Fern Hollow, Pittsburgh, and Moon Township, Allegheny County.

ADDITIONAL LOCALITY.

The writer has seen this species at Sandy Creek, Allegheny County, Pa.

REMARKS.

The Blue Crawfish is rather abundant in the region indicated by the above localities, and apparently represents a geographical differentiation of *C. carolinus*, the Red Crawfish. The points in which it differs from the latter species, aside from color, are slight, but are constant according to my observations.

The rostrum is markedly different from that of *C. carolinus*, although slightly variable. It always is smaller than that of the latter species and narrower, with less distinctly marked lateral angles. The lateral margins are swollen, but the swelling is less marked, and does not suddenly decrease at the lateral angles. The degree of convergence of the margins is variable, but generally much more pronounced than in the Red Crawfish; cases like that figured in Plate XXXIX, Fig. 4*b*, are rather rare, in fact, this case forms the extreme in this direction.

In the shape of the hand, the rounded outer margin and the absence of serrations on it are other striking characters of this species; and the carpopodite is distinguished by the larger number of spiniform tubercles, as described above. The outer lower margin of the meropodite generally has a blunt and smooth keel, with only one small tubercle near the distal end (which may be absent). Among my material I had only ten specimens which revealed an exception, where two such tubercles were present, and in only two of them were these tubercles present on both chelipeds. In the others they occurred only on one side. There are instances in which a large number are found, but always in claws which have been regenerated.

Aside from the slight variations indicated above only a few exceptional cases have been encountered in which marked deviation from the above description of the prevalent colors occurs. The blue ground-color is always present on the anterior part of the carapace and the chelæ. In a rare variation, which has been observed about half a dozen times, the ground-color of the posterior part of the carapace and parts of the abdomen are more or less purplish (*auricula-purple*, VIII, 3). Furthermore a single adult female was found at Monaca in which all red tints were absent; the blue of the body was very clear, the margins of the rostrum were blue like the carapace, the finger tips were whitish, all spines and tubercles were pure white, and the antennal flagellum was a pure blue. Specimens in which the margins of the rostrum have the same shade of blue as the carapace are not infrequent.

Other freaks are occasionally found, as for instance a specimen without an acumen on the rostrum, the latter being evenly rounded off; a specimen with the immovable finger of the left hand with a double tip, the outer one the larger, and a specimen with the movable fingers of both hands only half as long as usual, thick, short, and conical. Such cases apparently are due to some previous injury, and suggest nothing of special interest.

All the variations mentioned above are rare and are not restricted to certain parts of the range of the species, so that we do not distinguish any regional varieties.

7. CAMBARUS (BARTONIUS) DIOGENES Girard.

(Plate A, Fig. 3; Plate XXXIX, Fig. 11; Plate XL, Figs. 6 and 7.)

Cambarus diogenes Girard, 1852, p. 88; Faxon, 1884*b*, p. 144; Abbott, 1884, p. 1157; Faxon, 1885*a*, p. 71; Faxon, 1885*b*, p. 359; Faxon, 1885*c*, p. 140; Underwood, 1886, p. 368; Faxon, 1890, p. 624; Ortmann, 1891, p. 12; Hay, 1896, p. 489, Fig. 7; Faxon, 1898, p. 650; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20, 48; Hay, 1899, p. 959, 961; Harris, 1900, p. 267; Williamson, 1901, p. 11; Hay, 1902*a*, p. 235; Ortmann, 1905*a*, p. 398.

Cambarus obesus Hagen, 1870, p. 81, pl. 1, f. 39–42, pl. 3, f. 163, pl. 9; Smith, 1874, p. 639; Forbes, 1876, p. 5, 19; Bundy, 1877, p. 171; Bundy, 1882, p. 183; Bundy, 1883, p. 403.

Cambarus diogenes ludovicianus Faxon, 1884*b*, p. 144; Hay, 1899, p. 959, 962.

Cambarus dubius Osburn and Williamson, 1898, p. 21, (non *dubius* Faxon).

Cambarus (Bartonius) diogenes Ortmann, 1905*b*, p. 120, 135.

Body robust, smooth, except for short hairs, chiefly on the chelæ in fresh shells; the hairs also to a certain degree persist upon the hand and fingers in older individuals.

Carapace subovate, not depressed, but rather compressed. $G:H:B = 1:0.88$ to $1.0:1.06$ to 1.2; that is to say, the transverse diameter of the carapace is very slightly greater than the vertical, at the hepatic region sometimes even less. Greatest width of branchial regions well forward, not far from the cervical groove.

Cervical groove deep, not interrupted on the sides.

Areola distinctly longer than half of the anterior section of the carapace ($a:p = 1:0.61$ to 0.75), very narrow, and generally obliterated in the middle; that is to say, the two lines bordering the branchial regions are in contact in the middle of the carapace. In rare instances a small space is left between them, upon which there is no room for punctures.

Rostrum more or less lanceolate, rather narrow, but not very long, reaching hardly beyond the distal end of the second joint of the peduncle of the antennula, being often shorter. Upper surface slightly concave, with elevated margins. Margins not much swollen, the swelling gradually disappearing toward the tip, converging, straight, or slightly convex, contracted to form a short triangular acumen. Basal angles of acumen indistinct, rounded, without any trace of marginal spines.

Point of acumen short. Postorbital ridges short, terminated bluntly in front, slightly divergent posteriorly, ending in a low, indistinct swelling.

Surface of carapace punctate, slightly granulate on the hepatic region, and with a few granules on the branchial region, immediately behind the cervical groove. No lateral spine. External orbital angle present, distinct, angular or rounded, but without tubercle or spine. Branchiostegal spine formed by a small, often indistinct, tubercle.

Abdomen about as long as the carapace, or very slightly shorter or longer, narrower than the carapace in the male, markedly wider and about as wide as the carapace in the female. Anterior section of *telson* with 1–3 (generally 2) spines on the posterior lateral corners. Posterior section semi-elliptical, slightly wider than long, and about as long as the anterior section.

Epistoma similar to that of *C. carolinus* and *monongalensis*, comparatively long and narrow, rather flat, and with the anterior section semi-circular, semi-elliptical, or truncate and subquadrate, with or without median point, and about as long as wide.

Antennula with a small tubercle on the lower margin of the basal joint.

Antennal peduncle without spines or tubercles on the proximal joints.

Antennal scale small and short, slightly longer than the rostrum, and reaching to the base of the fifth joint of the peduncle of the antenna. Spine of outer margin strong; laminar portion not much wider than the spine, its inner margin parallel to the outer margin of the spine for a considerable distance.

Flagellum short, often only as long as the carapace or even shorter, never reaching beyond the second abdominal segment.

First pereiopods (Pl. XL, Fig. 6) stout and very robust in old individuals; not much different in the male and female, except for their very large size in old males. Hand ovate, broad, depressed. Surface punctate. Inner margin of palm convex, with two irregular rows of tubercles, and a few scattered tubercles on the upper surface near the marginal rows. Outer margin smooth, rounded proximally, slightly angular distally. Fingers at least one and one-half times as long as palm (the latter measured from articular tubercle with carpopodite to articular tubercle with dactylopodite), gaping at the base, straight both in young and old specimens. Cutting edges with a number of strong but irregular tubercles; one tubercle at about the middle of the edge of each finger is generally the largest. Outer margin of movable finger with more or less distinct tubercles at the proximal end. Upper surface of each finger with a low longitudinal rib, bordered by rows of punctures.

Carpopodite about as long as wide, shorter than palm, with a deep longitudinal sulcus above, and a few more or less distinct tubercles between sulcus and inner margin. A strong pointed spine in the middle of the inner margin, straight, and directed obliquely forward. A tubercle or spine on anterior margin of lower side, and a low tubercle at articulation with hand. A few additional tubercles may be present on the inner margin and the lower side, but they are very rarely spiniform.

Meropodite smooth, with 1–3 indistinct tubercles near the distal end of the upper margin. Lower side with an outer row of 1–4, and an inner row of 7–11 spiniform tubercles.

Ischiopodite of third pereiopods hooked in the male; hooks in the male of the first form strong, subconical.

Coxopodite of fourth pereiopods with a strong, slightly compressed tubercle.

First pleopods of male (Pl. XXXIX, Fig. 11) similar to those of *C. bartoni*, the tip of the inner part, however, tapering gradually to the point.

Annulus ventralis of female similar to that of *C. carolinus.*

Size. — The largest specimens at hand from the eastern part of the state are a male (first form) and a female from Ridley Park, both 83 mm. long. From the western part of the state I have a male of the first form from Nine-Mile Run, Pittsburgh, which measures 92 mm. in length, and a male of the second form from Millvale, Allegheny County, which is 93 mm. long. The largest female is from Nine-Mile Run, and measures 97 mm. in length.

In the west this species attains a much larger size. The maximum length has been recorded by Hagen, 4.5 in. = 115 mm. However, the Carnegie Museum possesses a male of the first form from Bluffton, Wells County, Indiana (collected by E. B. Williamson), which is now (in alcohol) 122 mm. long, but measured 124 mm. when alive.

Color (Pl. A, Fig. 3). — The color is rather variable within certain limits, but the ground-color is similar to that normally seen in crawfishes, brownish or greenish.

Ground-color on carapace and abdomen from *olive-green* (Ridgway, 1886, X, 18) to *raw-umber* (III, 14), *mummy-brown* (III, 10) and *ferrugineous* (IV, 10), shading on the sides through *drab* (III, 18) or *russet* (III, 16) to *fawn-color* (III, 22) and whitish. Margins of rostrum *rufous* (IV, 7) or *ferrugineous* (IV, 10). The hand is *tawny-olive* (III, 17) to *burnt sienna* (IV, 6) and *rufous*, shading to *olive-yellow* (VI, 16) toward the outside. At the bases of the fingers there is often a distinct shade of *olive-green* (X, 21). The finger tips are *rufous*, the tubercles of the hand *cream-buff* (V, 11) or *whitish.* The legs are *ochraceous-buff* (V, 10) with *olive-buff* (V, 11), or *russet* (III, 16) with *olive-green* (X, 18) at the joints. Lower side of body pale *rufous* or pale *orange-buff* (VI, 22), or *whitish.* The antennal flagellum is annulated dark *olive-*

green and *whitish.* The relative amount of green and brown changes very considerably with different specimens, but in general we may say that green prevails in the young, and brown in older specimens.

Color of newly laid eggs *buff* (V, 13); when more advanced *prune-purple* (VIII, 1), or *indian-purple* (VIII, 6) on one side, *cream-color* (V. 20), or *dirty-white* on the other.

In the Carnegie Museum there are altogether three hundred and twenty-three specimens of this species, of which twenty are from eastern and two hundred and sixty-six from western Pennsylvania. Two specimens are from Maryland, five from West Virginia, twenty-four from Indiana and three from Iowa; while one specimen is from each of the states of Delaware, Ohio, and Kansas.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: *Bucks County,* Penns Manor; *Philadelphia County,* Essington; *Delaware County,* Ridley Park; Marcus Hook; *Greene County,* Waynesburg; Rice's Landing; *Fayette County,* Smithfield; Dunbar; Pennsville; *Washington County,* Francis Mine near Burgettstown; *Beaver County,* Baden; Racoon Township; *Allegheny County,* Troup's Retreat, Moon Township, (E. B. Williamson coll.); Stowe and Neville Townships, (Atkinson, Graf, and Williamson coll.); Edgeworth, (Mrs. E. Courtney coll.); Westview, (D. A. Atkinson coll.); Millvale; Fern Hollow and Nine-Mile Run, Pittsburgh; Schenley Farm, Pittsburgh, (F. E. Kelly coll.); Silver Lake, Pittsburgh, (E. B. Williamson coll.); Bruce's Ice Pond, Pittsburgh, (Atkinson and Williamson coll.); Carnegie, (D. A. Atkinson coll.); Jack's Run, North Versailles Township; Rankin, (O. T. Cruikshank coll.); Squaw Run, near Aspinwall; Montrose; Harmarville; Russelton; between Gibsonia and Bakerstown Station; Thornhill; *Westmoreland County,* Donohoe; New Alexandria; Dundale; Reservoir of McGee Run, Derry; Blairsville Intersection; Livermore; Kiskiminetas Junction; *Indiana County,* Homer; Creekside; *Jefferson County,* Punxsutawney; *Armstrong County,* Long Run, Avonmore Station; Kittanning; *Butler County,* Renfrew; Branchton; *Lawrence County,* Wampum; *Mercer County,* Mercer.

DELAWARE: *Sussex County,* Seaford, (S. N. Rhoads coll., exch. Ac. Nat. Sci., Philadelphia).

MARYLAND: *Kent County,* Chestertown, (E. G. Vanatta coll., exch. Ac. Nat. Sci., Philadelphia).

WEST VIRGINIA: *Hancock County,* Congo; *Brooke County,* Colliers; *Wetzel County,* New Martinsville.

Ohio: *Franklin County*, Columbus, (E. B. Williamson coll.).

Indiana: *Wells County*, Bluffton; Twin Lakes; Craigville; Liberty Center; Uniondale; *Blackford County*, Hartford City; *De Kalb County*, Newville (all coll. by E. B. Williamson).

Iowa: *Greene County*, Cooper, (J. B. Hatcher coll.); *Lee County*, Denmark (R. L. Baird coll.).

Kansas: *Douglas County*, Lawrence, (S. Prentice coll.).

PREVIOUS RECORDS.

Type Locality: Washington, D. C., (Girard).

New Jersey: Trenton, Mercer County, (Abbott).

Maryland: Worcester County, (Faxon); Dorchester County, (Faxon); Caroline County, (Faxon); Baltimore County, (Faxon); St. Mary County, (Faxon).[27]

Virginia: Accomac County, (Faxon); Northampton County, (Faxon); Alexandria County, (Faxon); Prince William County, (Faxon); Fredericksburg, Spottsylvania County, (Faxon); Petersburg, Dinwiddie County, (Hagen).

North Carolina: Kingston, Lenoir County, (Faxon); Wilmington, New Hanover County, (Faxon).

Pennsylvania: Derry, Westmoreland County, (Faxon); Pittsburg, Allegheny County, (Williamson).

Ohio: Oberlin, Lorain County, (Osburn and Williamson); Knox County, (Williamson); Columbus and Lockbourne, Franklin County, (Faxon); Montgomery County, (Williamson).

Michigan: Detroit, Wayne County, (Faxon).

Kentucky: Louisville, Jefferson County, (Faxon); Bee Spring, Edmonson County, (Faxon); Mammoth Cave, Edmonson County, (Hay).[28]

Indiana: Kendallville, Noble County, (Bundy); Riverside, Laporte County, (Faxon); Kokomo, Howard County, (Faxon); Mechanicsburg, Henry County, (Bundy); Irvington, Marion County, (Hay); North Salem, Hendricks County, (Hay); Greencastle, Putnam County, (Hay); Bloomington, Monroe County, (Hay); Knox County, (Faxon).

---

[27] Faxon also gives Deer Park, Garrett County, (Coll. P. R. Uhler). I have doubted (1905*b*, p. 136) the correctness of this locality. In order to be sure I have asked Dr. P. R. Uhler of Baltimore to send to me the specimens upon which this record was founded, and Dr. Uhler very kindly complied with my request. There were two males of the second form and four females in the lot, all belonging to *C. bartoni*, and representing the typical form, with the exception of one male, which I have identified with the southern form of *C. bartoni robustus* (see above, pp. 391 and 393). Thus this record (Deer Park) for *C. diogenes* is to be dropped.

[28] The localities in Jefferson and Edmonson Counties are given by Faxon with a ?; but Hay's record of this species from Mammoth Cave tends to confirm their correctness.

ILLINOIS: Chicago, Cook County, (Hagen); Evanston, Cook County, (Hagen); Lawn Ridge, Marshall County, (Hagen); Abingdon, Knox County, (Faxon); Decatur, Macon County, (Faxon); Belleville, St. Clair County, (Hagen).

WISCONSIN: "Abundant in Wisconsin," (Bundy); Racine, Racine County, (Faxon); Green County, (Faxon); Appleton, Outagamie County, (Faxon).

MINNESOTA: Fort Snelling, Hennepin County, (Faxon).

IOWA: Davenport, Scott County, (Faxon); Delhi, Delaware County, (Faxon); Belmond, Wright County, (Faxon).

MISSOURI: St. Louis, St. Louis County, (Faxon); Carroll County, (Faxon).

KANSAS: Leavenworth, Leavenworth County, (Faxon); Lawrence, Douglas County, (Harris).

ARKANSAS: Paragould, Greene County, (Faxon); Fayetteville, Washington County, (Faxon).

MISSISSIPPI: Monticello, Lawrence County, (Hagen).

LOUISIANA: New Orleans, (Hagen).

WYOMING: Cheyenne, Laramie County, (Faxon).

COLORADO: Clear Lake, (Faxon)[29]; Boulder, Boulder County, (Harris)[30].

REMARKS.

Cambarus diogenes occupies two areas, in the United States, which, according to our present knowledge, are separated from each other; a western and an eastern. Both areas enter Pennsylvania, the one extending over a large portion of the southwestern territory of this state, the other being much smaller and restricted to the southeastern extremity.

I have closely studied the material at hand, and have found certain differences between eastern and western specimens, which however are very slight, and not always constant; yet a tendency to a morphological separation between the eastern and western forms seems to be indicated. Faxon (1885*a*, p. 72) has already called attention to some of these differences.

The description given above refers chiefly to the *eastern* form of this species. Specimens from western Pennsylvania show the following differences:

1. *Areola* in most cases not entirely obliterated. There are, indeed, cases in the eastern form where the two lines bordering the branchial regions are not in contact, but they are rare. In western Pennsylvania the latter condition is rather the rule, although specimens in which both lines unite, forming in the middle only one line,

---

[29] Location unknown to the writer.

[30] Professor T. D. A. Cockerell has sent to me for examination a young male collected October 7, 1905, in a small stream near Boulder. Although very small it clearly belongs to this species.

are by no means absent. There is some variability in this character. Generally a very narrow space is left between the two lines, which does not leave room for any punctures. But it is a curious fact that the areola is widest in specimens from Fayette and eastern Greene Counties. In these localities specimens with an entirely obliterated areola are exceedingly rare, and specimens with the areola so wide that there is room for one irregular row of punctures are rather frequent, (Pennsville, Dunbar, Smithfield, Fayette County; Rice's Landing, Greene County). Such specimens with punctures on the areola, which is accordingly wide, are scarcely found anywhere else. I possess only one from Pittsburgh.

2. *Rostrum*, in all eastern specimens at hand, with a more or less distinct acumen. In the western form there is a distinct tendency to render the acumen obscure. Indeed there are many specimens which have the acumen exactly as in the eastern form, but there are as many where it is not marked, the margins converging evenly to the tip. In such specimens the rostrum assumes a rather regular lanceolate shape, and appears somewhat more elongate and narrow. However, it is actually not longer than in the eastern form.

3. The swelling at the posterior ends of the *postorbital ridges* is sometimes more distinct in western specimens.

4. In our western form the *external orbital angle* is rarely angular, but generally blunt or rounded. In some cases it is very slightly developed.

5. There are specimens in western Pennsylvania where the posterior section of the telson is longer and more tapering. In extreme cases this is rather striking, the posterior section being distinctly longer than the anterior, and longer than wide. This latter condition is never found in eastern specimens. On the other hand there are many western specimens which do not differ in this respect from the eastern, and many transitional conditions have been observed.

6. *Antennal scale* in the western form often slightly wider than in the eastern, and with a stronger spine. This difference, however, is very slight.

7. *Chelæ* in the western form (Pl. XL, Fig. 7) of slightly different shape, but this difference always holds good, provided the chela has not been regenerated, and is otherwise normally developed. The inner margin of the palm in the eastern form has always two rows of tubercles, while on the upper surface there are at the best only a few minute, scattered tubercles, chiefly near the base of the dactylopodite. In the western form the two rows of tubercles are also generally distinguishable, but often the inner row is irregular, and merges into the scattered tubercles present upon the inner half of the upper surface. These latter tubercles are invariably present, and are much more numerous than in the eastern form. The dactylopodite

of the western form is generally shorter. While in the eastern form it is at least one and one-half times as long as the palm, in the western form this relation is the maximum, and is due to a proportionally heavier and stronger development of the palm as compared with the fingers. (This does not hold good for regenerated chelæ, in which the dactylopodite always is considerably longer in proportion to the palm.)

The tubercles of the cutting edge of the dactylopodite are slightly different in both forms. In the eastern the third or fourth is generally much larger, and, just before it, there is a gap, as if one tubercle were suppressed. This produces a distinct excision at the base of the finger, which is always more or less marked, even in rather young individuals, so that the fingers always appear gaping at the base (Pl. XL, Fig. 6). In the western form the fourth or fifth tubercle is larger than the rest, but there is no distinct gap anterior to it, the three or four proximal tubercles being rather equidistant. They decrease slightly in size from the first to the fourth, so that a slight emargination is indicated. But this emargination and the large tubercle following it are well distinguishable only in larger individuals; in younger specimens they are rather indistinct, or entirely wanting, so that the basal gap is absent, and the fingers are in contact all along their edges.

The differences in the relation of dactylopodite to palm, and in the tubercles of the dactylopodite, give to the whole chela of the western form a different aspect, the hand appearing rather more massive with shorter fingers. (See Pl. XL, Figs. 6 and 7.)

8. The *colors* in western specimens are more vivid, and with more contrast. Eastern specimens are more uniformly russet or olive-green, with no oil-green at the base of the fingers, while the latter tint is very characteristic of the western form, at least in specimens of a certain size. Old western specimens, when fresh, are rather brilliantly colored.

I think I am able to recognize and to distinguish eastern and western specimens, chiefly by the help of the characters of the chelæ, if the latter are normally developed; but I do not know whether it would be advisable to distinguish both forms by varietal names. The latter may be necessary in future, when the forms of *C. diogenes* from the regions west of Pennsylvania have been more closely studied. I think I am able to see certain differences in the western specimens in our collections, but the material is too poor to be sure of it.

No remarkable freaks or malformations have been observed in this species, with the exception of a few color variations. They are the following:

1. In Fern Hollow, Pittsburgh, a specimen was found in a stagnant pool, 6 to

10 inches deep, in yellowish brown mud. Its color was entirely yellowish brown, mottled lighter and darker, and no trace of olive-green was present. This apparently was a stray specimen.

2. A large male of the first form was found at Dunbar, Fayette County, the ground-color of which was *salmon-color* (VII, 17), the abdomen *buff* (V, 13), *whitish* on the sides. The red was brightest on the chelæ, with traces of green between the tubercles of the hand, and the lower side of the chelæ and body were dirty brownish yellow. This is apparently a case of albinism.

IV. ECOLOGY AND GEOGRAPHICAL DISTRIBUTION.

A. Ecology.[31]

Satisfactory conclusions as to the relation of geographical distribution to the physical conditions of the country can only be expected, if we know all about the ecological laws governing the different species. With reference to the seven species of crawfishes present in Pennsylvania, we shall see that the ecological conditions are quite varied, and the single species behave very differently. Thus it is necessary to discuss these facts first, before we attempt to study the distribution.

Three main types of ecological conditions may be distinguished among our crawfishes. We possess species which generally live in the larger rivers; other species which favor the opposite extreme, preferring the groundwater, where it is not far from the surface, and appears in the shape of springs and swamps; and intermediate between these two conditions is a species which selects the smaller streams for its home. We may conveniently call these "the river species," "the mountain-stream species," and "the burrowing species."

1. *The River Species.*

Cambarus limosus, *Cambarus propinquus*, *Cambarus obscurus*.

Although principally living in the larger rivers of the state, these species are not entirely restricted to them, being able to live in any larger body of water, running or stagnant, providing it is permanent. Thus these forms, in some cases, go far up stream into the smaller tributaries of our rivers, sometimes almost to their sources. The only condition which stops them in an up-stream migration seems to be the character of the watercourse, which must not be too rapid and rough. This is a very important fact, and largely explains the absence of these species in the mountainous regions of the state. On the other hand, these species are by no means averse to quiet bodies of water, such as ponds and lakes, and although the parts of Pennsylvania where these species are found are singularly free from lakes, crawfishes are almost regularly found in them, and even in artificial ponds, reservoirs, etc. It has been observed that in ponds and lakes these species seem to thrive exceptionally well.

---

[31] "Ecology," the science of the "relation of organisms to external conditions," is the oldest term, created by Hæckel ("Oecologie," in "*Generelle Morphologie der Organisme*," 1866). The term "Bionomics," which is often used in its place, was first introduced by E. Ray Lankester (in the article: Zoölogy, in Encyclopædia Britannica, 9th ed., 1888, p. 803), and subsequently, but independently, (as "Bionomie") by J. Walther (*Einleitung in die Geologie als historische Wissenschaft*" 1. Bionomie des Meeres, 1893, p. XX). The term "Oecologie" was revived chiefly by E. Warming, (Plantesamfund. Grundtræk af den økologiske Plantegeografi, 1895). The term "Ethologie" introduced by F. Dahl (Verh. Ges. Naturf. & Ærzte, Bremen, LXIII, 2. 1891. p. 123) has a wider sense, including also what we here call "life-history."

Among the three species belonging to this class, there are certain differences. *Cambarus limosus* of the eastern part of Pennsylvania has its main abode in the quiet streams of the lowlands. It goes up stream for a certain distance, but rarely, and only under exceptional conditions, (see below), is it found in streams which are somewhat rough. Its center, at least for this state, is in the lower part of the Delaware River, where it is under the influence of the tides. Here it prefers the muddy banks, living among the water weeds, and congregates often in large numbers at the mouths of small streams tributary to the river. In fact the latter places are the most favored, since this species loves to hide under stones, and it is chiefly at the mouth of streams that stones are found in this part of the Delaware. Further up stream, beyond the reach of the tide in the Delaware, and in its tributaries (Neshaminy Creek, Schuylkill River, Brandywine Creek) and in the Susquehanna and Potomac drainages, this species is generally found hiding under stones, as was first reported by Abbott (1873, p. 80) with reference to the Delaware River at Trenton, N. J. But such is not the exclusive habitat of *C. limosus.* It is very often found in quiet ponds, in ditches or canals, where there are no stones to afford concealment. In these places it frequents patches of weeds (*Vallisneria*, etc.), often in considerable numbers. From such places (ditches of the Delaware meadows at Trenton) it was reported by Faxon (1885*a*, p. 88). *C. limosus* is generally found in very shallow water, but sometimes at a considerable depth. I captured a few specimens in a quiet cove of the Delaware River at Penns Manor, Bucks County, at the woodwork of a pier, at a depth of from six to eight feet (Sept. 15, 1905), and frequently got numbers of it in creeks and canals (Schuylkill Canal, Manayunk; Delaware and Raritan Canal, Princeton), in the water weeds, at a depth of from two to four feet. Although this species loves to hide under stones, and although it scoops out the dirt under stones, it is by no means a burrowing species. The hollows made under stones are very insignificant, and I have never observed that it makes holes in the banks of streams. Faxon (1885*a*, p. 89) reports that Mr. Uhler found this species near Cumberland, Md., in "holes in the bottom and sides of a canal," but whether these were made by the crawfish, or were cracks and joints between stones, remains doubtful. In the lowlands in Maryland this species, according to the same authority, is found under stones in rivers and creeks. We may say of *C. limosus* that it is of all the species of this state the one which most decidedly prefers the quieter water of large rivers, canals, and ponds; that it likes to hide under stones, but is not at all averse to muddy bottoms and masses of vegetation.

The latter trait distinguishes it from the species of the western rivers, *Cambarus obscurus*, which dislikes muddy bottoms (without stones) and vegetation. In fact, this is so general a rule, that it is vain to look for *C. obscurus* in any part of a river which has no stones. Only in rare and exceptional cases have I found it not hiding under stones, apparently being forced to do so by necessity. I observed this in two cases: in the Allegheny River at Larabee, McKean County, and the Shenango River at Linesville, Crawford County. In both cases the river runs through peaty soil (through the Pymatuning Swamp at Linesville), and it was only after a long search that the species was discovered, when I struck places where stones were lying in the water. But it was interesting to note that at both places the supply of stones was apparently not sufficient to accommodate all the specimens, and so a number of them had to be content with a shelter afforded by the peaty banks, where they had built short, horizontal holes, not more than a few inches long, close to the edge of the water. These holes are apparently only temporary, and are often abandoned and changed, since a number of them were seen on the banks above the present water level, which were built and inhabited at a previous higher stage of the river. *C. obscurus* does not love vegetation. The patches of *Dianthera americana*, so frequent in our rivers, do not harbour many crawfishes, although they are not entirely absent from them; but they do not hide under these plants and their roots, but under stones. They always scoop out a hollow under the stone selected, and bring out the mud and gravel, throwing up a small rubbish pile in front of the hole, which, however, is soon obliterated by the current. The crawfishes are easily found by noting these rubbish piles. They rarely go into deep water (possibly only in winter), but always are close to the banks in shallow water; but on the other hand they never go out of water. In the mountains of western Pennsylvania this species is generally absent, and it is apparently the roughness of the streams which causes its disappearance. The stones, under which it hides, must be rather permanent in their position, and must rest upon a bed of mud, sand, or gravel, to afford congenial conditions. In the mountain streams the rocks are rolled over very frequently, not only at high stages of water, but also under ordinary conditions, and this apparently does not suit the tastes of this species, and may be even directly dangerous. Since the general direction of the migration of this species in western Pennsylvania was and is upstream, it is evident that falls and rapids in the mountain regions present effective barriers, In the ponds and lakes of western Pennsylvania, connected with the Ohio drainage, this species is very abundant, but here also it always selects stones under which to hide.

Cambarus propinquus is restricted to Lake Erie and the lake drainage. It lives in the tributaries of the lake, exactly under the same conditions as *C. obscurus.* In the lake itself it has been found on two occasions. Dr. D. A. Atkinson collected a number at Presque Isle in the bay, but particulars as to their habitat were not recorded. The only other specimen from the lake was collected by myself on the sandy and gravelly beach near Miles Grove, thrown out by the surf, but alive. It does not seem to be very abundant in the lake, or at any rate seems to favor only certain places, and we may presume that places with stones and rocks on the beach and not too much exposed to the surf are the proper localities in which to look for it.

Cambarus propinquus sanborni in Ohio and West Virginia is found under exactly the same ecological conditions as its representative forms in Pennsylvania.

Nothing was known hitherto as to the ecological habits of *C. obscurus* and *propinquus,* except the short notice of Hay (1896, p. 498), that in Indiana *C. propinquus* lives "in the smaller streams hiding under stones, concealed in short burrows along the banks, or resting quietly on the bottom."

2. *The Mountain Stream Species: Cambarus bartoni.*

Conspicuously differing from "the River Species," *Cambarus bartoni* favors the rough streams of the mountains, hills, and the uplands generally, and is absent from the large rivers. The size of the stream may vary. In fact it goes up to the very sources and is found in the springs. The amount of water may be very small. Indeed it is frequently found in streams which dry out superficially during the hot season. But in such cases water is always present at a certain depth. The varying and often scanty supply of water forces this species to accommodate itself to these conditions, and thus it has become to a certain extent a burrowing species. It always selects stones to hide under, and in larger streams with a permanent supply of water is satisfied to scoop out a hollow under the stone after the fashion of *C. obscurus.* But very often the burrows are more complex, consisting of a hole going down to a depth of a foot or even more. These burrows are found along the banks of the streams, and the opening is often not in the water, but away from it, but rarely more than a few feet. The deepest burrows are found in late summer and fall, when the small streams are almost or entirely dry. Then necessity compels the crawfish to dig deep to reach the underground water. I have observed burrows eighteen inches deep in a vertical direction (see Plate XLI, Fig. 1). Under these conditions a considerable amount of dirt (mud, sand, gravel), is removed from the hole, and this is piled up in more or less regular mounds at the entrance of the hole, often assuming the shape of "chimneys," which may be fully equal in size to those of the typical chimney-builders. Here we see the origin of this habit. *C. bartoni* is not an habitual chimney-builder, but is content to hide under stones and to scoop out shallow holes when the stream has plenty of water. But when the supply of water becomes scant it has to dig down to reach it, and the burrows and mud-piles are the natural consequences of the attempt of the crawfish to accommodate itself to these peculiar conditions.

The manner in which the burrows are constructed, and the "purpose" of the chimneys will be discussed below when we come to consider the true burrowing species, and it may be remarked here, that everything said with reference to the latter holds good also for *C. bartoni.*

The roughness of a stream presents no obstacle to the presence of *C. bartoni.* Indeed, it prefers small streams which descend in cascades and fall from the hillsides, provided the rocks lying in them are stationary enough. It goes to the very uppermost springs and is frequently found there associated with *C. monongalensis* or *C. carolinus,* and also may be found near *C. diogenes.* I have observed cases where *C. bartoni* occupied holes, which were apparently built by specimens of these other species, and am able to give the following instances. Digging for *C. monongalensis* at West Brownsville, Washington County, I found in a large and wide hole a female *C. bartoni* (with eggs). The individual was much too small for this hole. To all appearances an old (abandoned?) hole of *C. monongalensis* was here occupied by *C. bartoni.* Similar observations were made at Avonmore Station, Armstrong County, where in the swampy ground of the valley of Long Run a colony of *C. diogenes* was found, and several *C. diogenes* were taken. In two holes, however, a half-grown specimen of *C. bartoni* was found, and again these holes were much too large for them. This place was about fifteen yards distant from the stream in which *C. bartoni* was abundant. Another similar case was observed at Creekside, Indiana County.

Going down stream *C. bartoni* remains abundant, as long as the character of the stream is maintained; after that it becomes scarce, but it does not disappear entirely, and in western Pennsylvania is frequently found associated with *C. obscurus*, in eastern Pennsylvania with *C. limosus*. In the large rivers it is generally entirely absent, and, if found, it is at the mouth of small streams, or at places where there are springs on the banks. Here it becomes evident that temperature plays an important part. The mountain streams, which are the favorite haunts of *C. bartoni*, are characterized all the year round by a rather uniform, but comparatively low temperature. In winter the temperature of the water goes down to just above the freezing point, but generally remains slightly higher (in running water about 35°–40° F.); in summer the maximum of these streams rarely goes above 60°, and does so only temporarily for a few days, while in the larger streams it remains for weeks above 70°, and may go up to 80° or even more. (The temperature of the Ohio River at Baden, Beaver County, on August 26, 1905, was 78° F. on a comparatively cool day.) That it is temperature which affects distribution is evident in summer, when in western Pennsylvania in the warm water of the rivers *C. obscurus* is found, but where there are springs on the banks discharging perceptibly cooler water into the river, *C. bartoni* suddenly appears.

It may be mentioned that I once found this species under very peculiar conditions. At New Hagerstown, Carroll County, Ohio, I discovered numerous burrows in the black muck of a swampy meadow at the bottom of a small valley, which I took first for burrows of *C. diogenes*. But I was unable to get any *diogenes*, every hole investigated being occupied by *C. bartoni* (about half a dozen were taken). This part of the meadow was close to a hillside, at the foot of which were numerous springs with a few stones, also sheltering specimens of *C. bartoni*. On the other side of the valley, which was about 100 to 200 feet wide, was a small stream with sandy and gravelly bottom, and a few stones, where also a few *C. bartoni* were present. The largest number of specimens was present in the swampy meadow, which is rather exceptional, but finds its explanation in the scarcity of stones in this locality.

The variety *C. bartoni robustus* in general agrees with the typical form as concerns ecological conditions, especially in that it prefers rough, rocky streams.* However, it was found preferably in streams of a larger size, avoiding the smaller headwaters. As Williamson (1901, p. 11) puts it: "at the headwaters" (Squaw Run, Allegheny County, is taken as an instance) "*bartoni* is found; following down the stream *robustus* is noticed; then an occasional *obscurus;* till finally *bartoni* becomes rare and disappears; then *robustus* disappears; and further down *C. obscurus* is the only species."

Since those parts of the stream which are inhabited by *C. bartoni robustus* are always well supplied with water, this form does not need to make extensive burrows, and I have never observed regular chimneys.[32]

The ecological conditions under which *C. bartoni* occurs were to some extent previously known. Goodman (1833 (1842), p. 293) gives a good account of them[33] as observed in small streams near Philadelphia. According to Abbott (1873) it is found near Trenton, N. J., burrowing in the muddy banks of ditches and small streams, rarely of the river (Delaware). This, however, is not the usual condition, as we have seen above. Faxon (1885*a*, p. 63) says that it prefers cooler waters of mountain regions or uplands, living under the stones in clear streams and in springs, which is the usual condition under which it is found in this state. However, that there are variations in its habitat, occasioned by exceptional conditions, is seen from the case mentioned above from the state of Ohio, from Abbott's account, and from the observations of Dr. J. Sloan as reported by Faxon (*l. c.*), according to which, in southern Indiana, it is found in ponds and still water, not in running streams. This is, however, not always the case in Indiana, since, according to Hay (1896, p. 489) it is found in "springs and streams of clear running water, where it hides under stones or digs short burrows into the banks."

3. *The Burrowing Species.*

Cambarus carolinus, Cambarus monongalensis, Cambarus diogenes.

a. General habitat.

The burrowing species are always found at a certain distance from open water, although often in close proximity to streams, ditches, or ponds; but never, under normal conditions, *in* them. Exceptions are very rare, and only accidental, and found chiefly in the case of young individuals which have not settled down permanently, or of individuals which have been disturbed.[34] These species, however, always depend on the presence of water, but it is the groundwater which is inhabited by them, and thus they are found at places where the groundwater is near the surface, in springs and swamps. In order to reach the water these species have to dig a hole in the ground, which often goes down through a considerable amount of dry soil, but it is always filled with water at the bottom.

---

[32] Shufeldt (1896, p. 27) figures a chimney of *C. bartoni robustus* from near Washington, D. C. Why Shufeldt attributes this chimney to this form, I do not understand. He says that he studied burrows near Washington, "many of these were of *C. diogenes*, others were of *C. bartoni robustus*, which I found abundant in Montgomery County, Md." The specimen which built the chimney figured was not taken by Shufeldt, and he says that in the vicinity another burrow was opened which contained a *C. diogenes*. According to the description of the hole belonging to the chimney, it is too deep and complex to belong to *C. bartoni*, and I do not see any reason for not regarding it as belonging to *C. diogenes*.

[33] The crawfish hole, eight to ten inches deep, with a wider chamber at the end, under stones in a small stream, with the opening in the water, undoubtedly belongs to this species.

[34] A case where young specimens of *C. diogenes* were found in numbers in open water by Dr. D. A. Atkinson will be discussed below. (See V.) This case is also to be regarded as exceptional.

The three species belonging to this class differ slightly with regard to the selection of their localities. *C. carolinus* chooses the mountains, and is found in springy places on the highest parts of the Alleghany plateau. The most favored localities are high valleys with a "hard pan," that is to say a layer of stiff clay below, which serves to keep the groundwater within a few feet of the surface. In such places the surface is often apparently dry, but upon digging down fresh and clear spring-water is found at a depth of one to three feet, and the holes of this species go down to the "hard pan" in order to reach the water. *C. monongalensis* favors similar conditions, yet it does not live in the mountains, but on the foothills west of the Chestnut Ridge. (The physiographic classification of these features will be discussed below). In this region extensive valleys with clay bottoms are rarely found, and thus *C. monongalensis* is content with the more restricted deposits of clay found on the hillsides. Such localities, however, are very abundant in this region, and wherever there is a spring and a certain amount of clay this species occurs. It prefers the cool spring-water, and if the springs collect to form a small swamp, this species is found on its upper margin, not *in* the swamp.

C. diogenes does not haunt springs to the same extent as *C. carolinus* and *C. monongalensis*. It is sometimes found under similar conditions as the other two species, but generally at places where a spring or small stream spreads out to form a swamp. It is also abundant in swampy ground along the borders of ditches and streams, and in swamps formed in depressions of the valleys of the large rivers (abandoned ox-bows). In the formerly glaciated area of the state it prefers kettle-holes. Like *C. monongalensis* it rarely occurs in the soft mud of swamps, but generally along their borders, where the firmer ground affords a better chance to dig more permanent holes. In consequence of the habit of preferring swamps to springs, *C. diogenes* is generally found at a lower elevation than *C. carolinus* and *monongalensis*, where it comes into contact with them. The two last named forms occupy the region of the clear and cool spring-water, while *C. diogenes* appears a little further down stream, where the water is not so clear, and in summer not so cool. In and near swamps the water in the holes of *C. diogenes* is often stagnant and muddy (even sewage is not much objected to by this species), while in the holes of the other two species there is always fresh and clear spring-water bubbling up.

b. Shape of the burrows. (See Pl. XL, Figs. 8 and 9, Pl. XLI.)

The burrows of these species (and also of *C. bartoni*) are to a certain degree alike, although they are very variable in depth and shape, so that there is very little uniformity. Only a few features are common to them. From the more or less dry surface they go down to the groundwater, where there is generally a kind of a pocket or widened chamber (Pl. XLI, Figs. 5 and 6). The width of the hole corresponds to the size of its inhabitants. It seems that one and the same individual permanently uses the same hole, although one and the same hole may be occupied by different individuals in succession, for an old abandoned hole may be occupied by a young specimen. This happens chiefly in localities where the holes are much crowded. There are places where the ground is fairly honeycombed with them,[35] and under such conditions a new hole may interfere with an old one, when a young specimen after attaining the proper size begins to build its own burrow, as it invariably does. If the old hole is abandoned the young specimen may take advantage of it, while in the alternative case, a fight ensues which ends in the expulsion or destruction of the weaker.

Each hole is always occupied by *one* individual only, with two exceptions. The first is the case of mating couples, when one adult male of the first form and one female are found in one and the same hole. The second is when the young of a certain size are associated with the mother in the hole of the latter.

The holes have all manner of shapes (see Pl. XL, and Pl. XLI). They may consist of a single shaft only, or may be more complex, branching off in various directions, and may have more than one opening at the surface. The chamber may be well marked or indistinct, and there may be several chambers. The chambers may be simple widenings of the hole, or may form side pockets. The direction of the descending shaft is rarely more or less vertical, and if vertical in the upper part, it generally soon assumes a slanting direction, and sometimes it is irregularly spiral. Shorter or longer branches may go off at the sides, and these may end blindly or may ascend to the surface. At the bottom side-branches may be absent, or may be developed to a considerable extent, running either horizontally or vertically. On steep hillsides, or along the banks of ditches, the general direction of the burrows is very often horizontal, the outward opening being lateral (Pl. XLI, Figs. 2, 3, 7).

The depth of the holes depends on the distance of the level of the groundwater from the surface. The holes are driven down by the crawfish to such a depth that a good supply of water is at the bottom at all seasons. Where the water appears at the surface, or is very near to it, the holes are sometimes hardly a foot deep. Generally they are considerably deeper, as much as two and three feet. They certainly at times go even deeper than this, but I never tried to dig at places where such conditions prevailed, that is to say, where from all appearances the level of the groundwater was more than three feet from the surface. Such conditions were not infrequently met with in the case of *C. carolinus.*

---

[35] I have seen this on the largest scale in the case of *C. carolinus* in the valley of Upper Decker's Creek near Reedsville, Preston County, W. Va. The whole valley, for two or three miles, offers favorable conditions for this species, and thousands of chimneys may be seen everywhere, coming up even between the railroad ties of the Morgantown & Kingwood Railroad.

In a general way we may say that the holes of *C. bartoni* are very simple (Pl. XL, Fig. 8; Pl. XLI, Fig. 1). Among the true chimney-builders the holes of *C. diogenes* are also rather simple, consisting often of a single shaft with a pocket at the bottom (Pl. XLI, Figs. 5 and 6). In *C. monongalensis* they are decidedly more complex (Pl. XLI, Fig. 2), and the highest degree of complexity is reached in *C. carolinus* (Pl. XL, Fig. 9).

The shape of the burrows of *C. diogenes* was first described by Girard (1852, p. 89), who called attention to their variable character. Tarr (1884, p. 127) has given sketches of burrows of this species, and also observed their variability. Of *C. carolinus,* only the fact that it is a chimney-builder was known (Faxon, 1885*a*, p. 71). The burrows of *C. monongalensis* (as *dubius*) were described by Williamson (1901, p. 12), and he emphasizes their complexity as compared with those of *C. diogenes.*

c. Construction of the burrows and of the chimneys.

Although the "chimneys" or mud-piles at the mouths of the burrows have often been described and their purpose discussed, (Girard, 1852; Tarr, 1854; Shufeldt, 1896; Harris, 1903), the manner in which the crawfish excavates the burrow and piles up the mud in front of it had never been correctly observed. Abbott (1885) describes how Mr. J. DeB. Abbott saw the crawfish (*C. diogenes*) engaged in building its chimney, and states that it comes out of its hole "bearing on the back of its right claw a ball of clay mud, which by a dexterous tilt of the claw was placed on the rim of the chimney." This description, as we shall presently see, is apparently founded upon correct observation, but the observer witnessed only the final act, and drew from it a wrong inference. The old observation of Goodman (1833, (1842), p. 293), that *C. bartoni* brings out of its hole an "armful of rubbish and throws it over the side of his cell, and down the stream," should be quoted, since, although referring to another species, it is pertinent and applies well to the regular chimney-builders as regards the mode of carrying the mud.[36]

---

[36] The way of carrying the mud out of the holes seems to be identical in all burrowing species. It has been observed in a similar form by Mr. W. S. Sutton in *C. pilosus* Hay, as described by Harris (1900, p. 272). That the crawfish uses

I have repeatedly observed the digging and the removal of the dirt out of the burrow. Of course it is impossible to see the digging going on in the field inside of the burrow, and consequently this was observed in the laboratory in the case of specimens of *C. diogenes* and *monongalensis* kept in captivity in large glass jars partly filled with clay and water. It is not difficult at all to see them at work, and after they have been brought into the laboratory the specimens begin to work within a short time, digging out the mud, carrying it upward and plastering it all over the walls of the jar. After some time (days or weeks), their activity lessens, and not much digging is done, producing the impression that they have become discouraged in the effort to construct something similar to the burrows in the field.

In digging the chelæ of the first pereiopods are used. The fingers are slightly spread out, so that they are about parallel, thus acting as forks for digging. They are pushed vertically down into the mud on both sides at the same time, and a lump of mud is thus loosened and lifted upward toward the ventral face of the body. In lifting the chelipeds are bent toward the body (the region of the mouth), and finally the ball of mud is appressed to the anterior part of the body and held in position by the chelæ. Very likely also the third maxillipeds take hold of it, but it was impossible to ascertain this. In this position, as Goodman expresses it, carrying an "armful" of dirt (or rather two armfuls), the crawfish walks slowly and deliberately to the mouth of the hole. I have repeatedly observed it coming out in nature.[37] It advances to the top of the chimney and deposits the mud pellet upon the rim, finally pushing it into the proper position with the upper (outer) surface of the claws. This latter act apparently was seen by Mr. J. DeB. Abbott; but according to my experience the mud is not brought up upon the back of the claw, but held, as described above, between the folded claws and the anterior part of the body.

After having been disturbed in the field, the crawfishes often begin to work again within a short time, and it is chiefly on such occasions that I have seem them at work, with the exception of one case, when I saw a large male of *C. diogenes* at work on the evening of April 30, 1905, (Sunday), in Nine-Mile Run, Pittsburgh. The

---

the "lateral tail-fins and telson" in any way, as suspected by Shufeldt (1896), in the sealing up of the orifice of the burrow, is hardly possible.

[37] The following particular instances may be mentioned: *C. bartoni* in a spring near Burgettstown, Washington County, Aug. 4, 1904; *C. carolinus* at Indian Creek, Fayette County, July 11, 1904; at Ohiopyle, Fayette County, July 12, 1904; at Myersdale, Somerset County, August 11, 1904; *C. monongalensis* in Fern Hollow, Pittsburgh, May 6, 1904; at Edgewood Park, Allegheny County, May 9 and 21, 1904; April 21, 1905; Monaca, Beaver County, June 30, 1904; at Cheat Haven, Fayette County, September 6, 1904; at Cameron, Marshall County, W. Va., May 1, 1905; at Morgantown, W. V., May 16, 1905; *C. diogenes* at Dunbar, Fayette County, September 7, 1904; in Nine-Mile Run, Pittsburgh, April 30, 1905.

usual time for working seems to be at night, and I have repeatedly observed that holes and chimneys disturbed or destroyed on one day exhibited signs of recent action on the following day. The crawfishes also seem to work occasionally on rainy or cloudy days; at all events, on such days it is easier to induce them to come to the mouth of the hole.

As to the purpose of the "chimneys," different opinions have been expressed. Abbott (1884) believes that the chimneys are designed, and that the crawfish intends to build just such structures, that is to say, rather regular subconical mud towers. He maintains this against Tarr's view (1884, p. 127), that the chimneys are not a necessary part of the burrows, and that they simply are the result of the digging. Subsequent writers have rather inclined towards Tarr's idea, for instance Shufeldt (1896, p. 89), who says that it is easier for the crawfish to build a chimney than to carry the mud away from the hole, and that "it is the most convenient and safest way to get rid of the pellets, besides being the least troublesome, and the method by which they are the least likely to roll back into the burrow." Harris (1903, p. 605) thinks that the chimneys very likely are only "the result of the easiest method of disposing of the material removed in excavating the burrow."

I must indorse the latter opinion, and for the following reasons. Regular chimneys, although claimed by Harris (*l. c.*) to be "usually" present and well built, are by no means so frequent as believed by most authors. Of course they are abundant in each colony of chimney-builders, and attract the attention of the observer. However, according to my experience well built chimneys are rather scarce compared with the total number of holes existing in a particular locality. In the majority of cases only more or less irregular and shapeless mud-piles are found at the mouths of the holes, and it is only under certain favorable conditions that they assume the shape of "chimneys." These conditions occur when the upper part of the hole is more or less vertical (see Pl. XL, Fig. 9 at *A*; Pl. XLI, Fig. 2 at *C*; Figs. 7 and 8), so that there is opportunity for the crawfish, in bringing up the pellets of mud, to deposit them rather uniformly all around the rim of the chimney. Supposing that it is always the lowest part of the rim at which additional pellets are deposited, which is altogether a very likely supposition, if the crawfish wants to get rid of the pellets as quickly as possible, the chimney must grow regularly. If, however, the mouth of the burrow opens in a slanting direction or horizontally, more or less one-sided mud-piles will be the result. (See Pl. XLI, Fig. 2 at *A*; Figs. 3 and 4). Further, much depends on the character of the material brought up. If it is fresh clay (not disturbed before), as will generally be the case when the crawfish is digging out a new hole, the pellets will be firmer, stick better to the rim of the chimney, and will remain in position, thus favoring the construction of a "well-built" chimney. On the other hand, when the mud is very soft, chiefly so when the crawfish is not digging new holes, but only cleaning out the old ones, the pellets are not firm, and the more liquid mud will flow down the outside of the chimney and render it lower and broader and, consequently, less "well-built." This latter fact also explains why young specimens often construct the neatest and most elaborate chimneys (Abbott). Young specimens, when they begin to work, bring out undisturbed, firm, and sticky clay, and the pellets are more likely to remain where they are placed on the rim of the chimney, which thus becomes very regular. Old specimens, on the contrary, live in holes which are practically finished, and when they work it is rather a process of "housecleaning" than of "housebuilding." The mud removed is more liquid and less sticky, and thus the chimneys are shapeless and irregular.

Very often the opening of the chimney is found closed. Abbott believes that the closing is merely the result of the accidental falling in of the rim. This may indeed happen, but in other cases it is plain that the crawfish closes the aperture intentionally, and Girard (1852) regarded this as the completion of the work of chimney-building. Shufeldt and Harris likewise believe that the crawfish itself seals up the burrow. This is my own opinion, and with Girard I think that the sealing up is the final act characterizing the completion of the burrow. Sealed burrows are very often found (see Pl. XL, Fig. 9; Pl. XLI, Figs. 2, 3, 4), chiefly in summer and fall, and it is in many cases evident, by the material used (see Pl. XLI, Fig. 6) that the shutting up was done by the crawfish by depositing pellets in the orifice. Often the "stopper" is not at the orifice itself, but a certain distance (5 to 6 inches) below. In fall the stopper is made rather substantially and fills the upper end of the hole for a distance of 6 to 10 inches (see Pl. XL, Fig. 9*b* at *D*), and such a filling cannot be accounted for by accidental falling in.

In my opinion the construction of the hole is the chief aim for which the crawfish works. For the removal of the clay and dirt an opening on the surface is needed; but when the burrow is completed this opening is shut up again, and the crawfish is content to remain inside, possibly for weeks or even months. This affords protection for the crawfish and its young from enemies (snakes). Females with eggs or young are almost always found in closed holes. It also affords necessary quiet and seclusion during the moulting process (soft shells are generally found in closed holes). It furthermore protects the hole from the disturbing influences of rain and frost. Of course it would not be advantageous to have the hole permanently sealed, since the crawfish wants to get out now and then (for mating, for food), but this is necessary only at long intervals (even for food it is not absolutely imperative to go out frequently, see *infra*), and the stopper is easily removed. During winter a more effective stopper is provided by the crawfish, and it remains for three or four months shut up in its hole.

The chief activity in chimney-building is in spring.[38] During winter frost destroys or damages the upper parts of the hole, and the rebuilding necessitates a good deal of work, and large mud-piles are accumulated in consequence (4 to 12 inches high, 12 to 18 inches in diameter). But after the hole has been restored to a satisfactory condition work ceases, and in summer not much fresh mud is brought out. Occasionally new chimneys are seen in summer, and the activity may be resumed at any time if necessary. Besides young specimens remain active all through the summer. In *C. diogenes*, as we shall see, it is chiefly in midsummer that the young begin to build their own holes. In the other species this may take place at any time from spring to fall, and thus the new and often very regular chimneys of small specimens may be seen at any time during the warm season.

General activity again begins with older specimens late in the fall, and this has a very interesting cause, and my attention was called to it by Mr. F. E. Kelly of Pittsburgh, but I have confirmed it by subsequent observations of my own. It is evident that the deepest parts of the holes are occupied and used by the crawfishes only in winter; these parts go down to about three feet, and thus are entirely out of reach of the frost. In summer these parts are abandoned and the crawfish inhabits only the upper parts of its burrow. In digging for crawfish in summer I often followed the main hole to a considerable depth, finally discovering that this hole was filled with soft ooze and mud, and that no crawfish was in this part; further careful investigation generally revealed a side branch at a higher level, which was clear of mud, and here the crawfish was captured. In the fall the deeper, abandoned part of the hole (see Pl. XLI, Fig. 7 at *c*), which fills up during the summer with dirt, forming at the bottom of the hole a soft, pulpy mass, is reclaimed by the crawfish in order to go deeper down out of reach of frost; the mud is consequently removed, and the necessity of cleaning out these deeper parts of the hole is the cause of the renewed activity in the autumn (Pl. XLI, Fig. 7). Before Mr. Kelly communicated to me his discovery of this fact I had not paid attention to it, but was able to verify it in the summer and fall of 1905. The fall activity takes place in the month of November (in the neighborhood of Pittsburgh), after the first killing frosts.[39]

---

[38] Young specimens begin first, as soon as the frost is out of the ground. New chimneys of *C. diogenes* were seen on March 23, 1905, in Nine-Mile Run, and the activity was general on April 6, 1905, (Renfrew). The first signs of new chimneys of *C. monongalensis* were seen at Edgewood Park on March 18, 1905 (frost only partly out of the ground); the activity was general on March 31, (Colliers, W. Va.), and April 4 (Edgwood Park).

It is evident from the foregoing observations and considerations that the "chimneys" are not necessary parts of the burrows. They are simply the result of the work of the crawfish, and only represent the material removed from the holes, which must be carried somewhere, and is most conveniently disposed of right at and around the mouth of the hole. The regular shape of the chimneys is simply due to the way the crawfish has to work under certain conditions, and to the physical properties of the clay.

Nevertheless there are certain advantages connected with the shape of the chimneys, which, however, are by no means always present, and, in my opinion, are not originally intended. The uppermost part of the hole generally has the tendency to be more or less vertical; an addition of 4 to 12 inches adds so much to the length of the vertical canal, and the crawfish, when sitting at or near the mouth, is able to suddenly drop down to escape enemies, which, as I have repeatedly observed, it actually does. Thus a considerable length of the vertical part is decidedly advantageous, giving the crawfish a chance to get more suddenly and effectually out of reach of danger.

Another effect of the mud-pile is noticed when the hole opens horizontally on sloping ground (banks of ditches). Here the mud-pile generally is semicircular, convex toward the ditch, concave toward the mouth of the hole, and thus serves to keep the water at a uniform level in the hole (Pl. XLI, Figs. 2 and 3), for generally in such cases the hole has spring-water flowing out of it. This may be advantageous under certain conditions, since I have often found that by removing a pile of mud of this character I was able to drain off the water from a considerable part of the hole, thus making it distinctly uncomfortable for the crawfish, as is evidenced by the fact that it often came out of the hole, as if to investigate the cause of the sudden disappearance of the water.

[39] In 1905 it began rather late. On November 8, in Fern Hollow and Nine-Mile Run, no fresh chimneys were seen on the golf links, where *C. diogenes* is abundant. On November 22 fresh mud-piles were numerous at the identical locality, several sharp frosts having occurred in the meantime. The same dates and the same facts were ascertained for *C. monongalensis* in Fern Hollow. Mr. Kelly's observations were made November 14 and 15, 1904, but in 1904 I noticed fall activity as early as November 5 (Nine-Mile Run, *C. diogenes*). (See Pl. XLI, Fig. 5.)

B. Geographical Distribution.

(Plates XLII and XLIII.)

1. *Cambarus limosus.*

a. Summary of Facts (see above, pp. 356–358).

This species belongs to the rivers, ponds, and canals of the lowlands of the Atlantic Coastal Plain and the Piedmont region[40] in the states of New Jersey, Pennsylvania, Maryland, District of Columbia, and Virginia. It has not been reported from the State of Delaware, but must certainly occur there also.

In Pennsylvania it extends up the rivers to a certain distance and in the Susquehanna River enters the Alleghany Mountain region. In Maryland it goes up the Potomac River, reaching the eastern extremity of West Virginia, thus also entering the Alleghany Mountain region.

Thus it is found in Pennsylvania in the drainages of the Delaware, Susquehanna and Potomac Rivers; but it decidedly prefers the region of the lower Delaware, from the bend of the river at Trenton downward. Here it is exceedingly abundant, as also in the lower and quieter parts of the Schuylkill River at Philadelphia. It goes up the Delaware and Schuylkill, and is found in their tributaries within the Piedmont region, but here it is by no means as abundant as in the Delaware. It seems to be absent in the great Alleghany Valley between the Susquehanna and the Delaware, but reaches the foot of the Blue Mountain between the Susquehanna and Potomac, occupying the Cumberland Valley (part of the great Alleghany Valley), and in the Susquehanna and Juniata it ascends even further, far into the Alleghany Mountains (Center and Bedford Counties).

b. Origin of the distribution of C. limosus.

In Pennsylvania.

In the Delaware River above Trenton this species goes up as far as New Hope in Bucks County; but is very rare there, (only one specimen was secured by the writer after a prolonged search), and it seems that it does not go far beyond this point, if at all. Professor A. E. Davison informs me that it is not found near Easton, Northampton County, about ten to fifteen miles from the Blue Mountain, and I was unable to find it in the Little Lehigh Creek near Emaus, Lehigh County.

---

[40] As to the division of Pennsylvania into *Coastal Plain*, *Piedmont Plateau*, *Great Alleghany Valley*, *Alleghany Mountains* and *Alleghany Plateau*, see Davis, 1889, p. 187, and Hollister, 1904, p. 10, map, Fig. 1; also Powell, 1896, p. 73 *et seq.* and map, and Willis, 1896, p. 169.

Mr. W. R. McConnell mentions (in his notes) the absence of crawfish in the Delaware at Portland, Northampton County.

It is found, however, in small tributaries of the Delaware in the southeastern half of Bucks County (Neshaminy Creek). In the Schuylkill River it goes up to Reading (Girard and also McConnell), and slightly beyond (Maiden Creek) in Berks County, but I have not been able to find it in the Schuylkill, where it comes out of the Blue Mountain, (Shoemakersville). It has been reported from Brandywine Creek in Chester County.

It is known from a number of places in the drainage of the Susquehanna, but they are all in the region of the Great Alleghany Valley or the Alleghany Mountains. I was unable to find it in the Susquehanna in Lancaster and York Counties, (Pequea and York Furnace), and I do not think that it is present there on account of the roughness of the river, which flows over a rocky bed in a channel cut deep into strata, chiefly of the archaic age, belonging to the Piedmont Plateau, from York Haven to the Maryland state-line and beyond. Such conditions are decidedly unfavorable for this species, and it is rather strange that it should be found at all above this rough part of the Susquehanna, which is about thirty to forty miles long. I think that this species immigrated into these parts in very recent times by way of the Susquehanna and Pennsylvania canals, which closely followed the river from its mouth in Maryland to the New York state-line and the Juniata up to Hollidaysburg, and connected it with the Schuylkill. These canals were maintained and in use a long time, beginning as early as 1834, were abandoned about 1890,[41] and at present only remnants of them are seen. *C. limosus* is often found in canals. First reported by Faxon from near Cumberland, Maryland, I have found it in considerable numbers in the Schuylkill and Delaware and Raritan Canals. It is quite possible that the Susquehanna and Pennsylvania Canals afforded this species the means of reaching the Susquehanna River in the region of the Great Alleghany Valley south of Harrisburg. Its further distribution up stream is then not strange, after the rough portion of the lower Susquehanna had been overcome, or avoided.

The same may be true of the Schuylkill River. Although certainly originally present in the lower part, it was the Schuylkill canal (once connected with the Pennsylvania canal) which possibly afforded an opportunity for *C. limosus* to go up the river as far as it does now, since the Schuylkill above Philadelphia is rather rough.

---

[41] The main line of the canal was completed in 1834, the Susquehanna Canal from Columbia to Havre de Grace in 1840; see Jenkins, 1903, pp. 275, 277, 282 and Klein, 1900, p. LXXIX; see also Hoyt & Anderson, 1905, p. 24. In the latter paper fine views of the scenery of the lower Susquehanna are published (Pl. 1, B, Pl. 8), which convey a good idea of the roughness of the water of the river.

Similar conditions seem to have played a part in the distribution of this species in the Potomac River. It has been reported from an old canal (Chesapeake and Ohio) four miles south of Cumberland, and I have found it in the Potomac at Cherry Run, West Virginia, and at South Cumberland. At both places it was scarce, and I am much inclined to believe that in this region (western Maryland and eastern West Virginia) it got into the river from the canal. Originally its distribution in Maryland was very likely similar to that in Pennsylvania, belonging only to the Coastal Plain and the Piedmont Plateau.[42]

Of the tributaries of the Potomac in southern Pennsylvania those which empty into the Potomac east of the Alleghany Mountain region also possess this species. It has been found in the drainage of the Monocacy River at Gettysburg, Adams County, and that of the Conococheague Creek in Franklin County, the latter locality again belonging to the Great Alleghany Valley. Further west, within the Alleghany Mountains, it seems to be absent. I did not find it in Big Cove Creek and Tonoloway Creek, Fulton County, and it is not in the collections made by Mr. H. A. Pilsbry for the Philadelphia Academy in Sideling and Town Creeks, Washington and Alleghany Counties, Maryland. This supports the view that the presence of this species in the Potomac as far up as Cumberland is due to the existence of the canal. Above Cumberland, where the canal ends, *C. limosus* is positively absent in the Potomac drainage in Pennsylvania as well as in Maryland and in West Virginia.

Thus it seems that *C. limosus* belongs originally only to the larger rivers of the southeastern section of our state, and that its real center for Pennsylvania is the Delaware. It has spread, however, upstream, and has approached the Alleghany Mountain region, even entering the latter in the Susquehanna River. This upstream dispersal is apparently not everywhere due to natural migration, but has been favored in recent times by canals. The present northwestern boundary, disregarding the Susquehanna River, is marked by a line (see Pl. XLIII) running from New Hope, Bucks County, to Maiden Creek and Reading, Berks County, thence to Bainbridge, Lancaster County, Carlisle, Cumberland County, and to Williamson, Franklin County. This line, generally speaking, runs parallel to the Blue Mountain, and it is very likely that the differences in the physical features of the Piedmont Plateau and the Alleghany Mountains have something to do with the distribution of this species, although the real cause cannot any longer be clearly seen, the original conditions being apparently obscured by several factors. For it should not be forgotten that the streams from the Susquehanna to the Delaware, issuing through the Blue

---

[42] The Chesapeake and Ohio Canal forms a continuous waterway from Washington to Cumberland, and was completed in 1850, see Hulbert, 1904, p. 160, and map opposite p. 80.

Mountain from the Anthracite basin, are largely charged with mine-water, and in this section of the state (Berks and Bucks counties) we see that *C. limosus* does not so closely approach the Blue Mountain, while in Cumberland and Franklin Counties, where the streams are clear, it goes to the very foot of the mountain.

Of course we cannot any longer ascertain what the original conditions were, and thus it is hardly profitable to enter into any further speculations. It is probable that the original range of this species has been reduced on the one hand by pollution of the streams, and has been extended on the other hand by modern river improvements. How far this holds good in detail, remains doubtful.

General origin of the distribution of C. limosus.

Aside from the more recent dispersal of this species just discussed, we are prompted to inquire how this species was able originally to reach the parts where it is now found.

As the writer has pointed out in a former paper (1905*b*, p. 108, 111, 114, 127) *C. limosus* stands rather isolated geographically as well as morphologically. It belongs to an ancient group of the subgenus *Faxonius*, probably the most ancient, which consists of five species. The other four species are entirely removed geographically from *C. limosus*, and are found in the central basin of the United States, in Kentucky, Indiana, and Missouri, that is to say, about four hundred miles to the west of the range of *C. limosus*, with the Appalachian System between them. We have to deal here with a marked case of discontinuity of distribution in the *limosus*-group. Since, as has been shown by the writer in the paper referred to, we locate the center of the subgenus *Faxonius* in the central part of the Mississippi drainage, *C. limosus* must have reached its present home by migration, and there are several ways by which it may have gone.

The most direct route is across the Alleghany Mountains. We may suppose that the *limosus*-group once extended in the Ohio drainage up into western Pennsylvania and West Virginia, and that it was able by some means to cross the divide into the Atlantic drainage. This does not appear impossible, inasmuch as in the mountains stream-piracy has taken place on a large scale during all ages (Davis, 1889). In fact all of the larger rivers now running into the Atlantic have captured large tracts originally belonging to the interior drainage, and the divide has been continuously shifted westward.

On the other hand, considering the ecological peculiarities of *C. limosus*, this assumption does not appear very likely. The habit of living in larger streams in rather quiet water would not favor a migration across the mountains, and if this form actually came by the way indicated some traces of its former existence should have been left in Pennsylvania, Maryland, or the Virginias, chiefly since there was no competition by any other species, river-forms being absent in the Alleghany Mountain region. Thus the direct route across the mountains seems to be out of the question, and this is further rendered probable by another consideration.

C. limosus being ancient, its migration eastward must have taken place at a remote epoch, certainly at an earlier time than that of a group which is more advanced, namely, the *propinquus*-group. As we shall see below, the latter existed already in Preglacial times, and thus we are forced to place the origin of the *limosus*-group at least as far back as the Tertiary. During this time, however, *the Ohio in its present form did not exist.* There was Spencer River,[43] in West Virginia and western Pennsylvania, and another river (Old Kanawha)[44] in West Virginia and Ohio, running northward to the Erigan River, which transversed the basin of Lake Erie.[45] And further the present upper Susquehanna (North Branch) is apparently new. It must have taken in Preglacial times a northward route toward the St. Lawrence basin, possibly also to the Erigan River (White, 1896, p. 376). All these rivers flowing northward in Pennsylvania and Ohio were different in character from what the rivers of this region are now. Their fall was slight, and they were rather sluggish. This is positively known of the Spencer River (or the Old Monongahela), which must have been practically at base-level (White, 1896, p. 377). If this was the case, nothing is opposed to the assumption that *C. limosus* (or its ancestral form) once was an inhabitant of some of these rivers. But then we see that its eastward migration cannot have been in a direct route, but must have gone on in a roundabout way, chiefly by the old Erigan River.

If the Erigan River was tributary to the Mississippi system, this is easy to imagine. If it drained to the St. Lawrence Gulf, as Spencer believes, we must assume an earlier crossing of the continental divide by this form, wherever this was situated (Indiana?), and then again a crossing of the divide between the Erigan River and the Atlantic coast drainage.

Be this as it may, we are forced to move the old range of the *limosus*-group to the north, into the Erigan River drainage, and this gives us the means of explaining the discontinuous range of this group. If it were at one time present in an area extending from Kentucky and Indiana through Michigan into Ontario, and if we assume that it crossed over into the Atlantic drainage somewhere in northern Pennsylvania or New York, the advancing ice of the Glacial Period must have entirely covered a large part of this range. In the central parts, in Ohio and western Pennsylvania, it was impossible for these forms to retreat southward, these parts being occupied by another vigorous group of river-crawfishes, as we shall see below (*propinquus*-group), and only in the east and west a chance to survive was left. The eastern remnant is the present *C. limosus*, the western is the group of species found now in southern Indiana and Kentucky.

---

[43] See Foshay, 1890, p. 368; Leverett, 1902, p. 89.

[44] See White, 1896, p. 376; Leverett, 1902, p. 100; Tight, 1903, map, Plate I, Plates 16 and 17. (Teays River.)

[45] See Spencer, 1881, map 2, and 1894, p. 293.

How *C. limosus* reached the Atlantic Coastal Plain from the Erigan basin is very hypothetical. One suggestion may be made. Not only does the North Branch of the Susquehanna seem to be a reversed river, but the West Branch has captured a large part of the original drainage of the Alleghany Plateau in Potter, Cameron, and Clearfield Counties. Davis (1889, p. 248) believes that this happened largely in Pretertiary times, since he thinks that the Alleghany Plateau belongs to the Cretaceous peneplain. However, Campbell (1903, p. 280) has shown that there are two old base levels in northern Pennsylvania, an older one (Cretaceous), identical with that of Davis, and a younger one (1,600 to 2,200 feet) corresponding to the Harrisburg peneplain of Old Tertiary age. Since the headwaters of the West Branch of the Susquehanna are carved into this second peneplain, it is probable that during Tertiary times the stream-piracy of the Susquehanna was going on rather vigorously. If we assume that *C. limosus* in Tertiary time existed in this part of the Erigan River drainage, namely in the Old Upper and Middle Alleghany Rivers,[46] which did not belong to the Old Monongahela or Spencer River, it must have been possible for it to get into the Susquehanna drainage in consequence of this stream-piracy in Tertiary times. This, however, is a mere suggestion. There is no other evidence for it but the bare fact that stream-piracy has gone on in this region. I mention it here only to show that the crossing over of this species into the Atlantic drainage is not altogether unthinkable.

After arriving in the coastal plain *C. limosus* was cut off in the Glacial Period from its allied forms in the west. But it survived, and in Postglacial times was able to advance again. But the Postglacial dispersal cannot have amounted to much, since the increasing roughness of the streams, caused by the Postglacial elevation of the country, was not favorable to a northward expansion. We do not know the exact northern boundary of *C. limosus* outside of our state. It is found in New Jersey as far north as Morris County, yet we do not know whether it reaches Raritan and New York Bays, and the Hudson River. No positive record from New York State is at hand (see De Kay, 1844, p. 23, and Paulmier, 1905, p. 117).

[46] See: Carll, 1880, pp. 333 and 336, map, Pl. 2; Leverett, 1892, pp. 129 and 132; Tight, 1903, map, Pl. 1.

An alternative supposition might be entertained. *C. limosus* might have arrived in its present home coming from the south by way of the Atlantic Coastal Plain. This, however, does not seem probable. First of all, the distribution of *C. limosus* does not extend southward beyond Virginia, and even in Virginia it is known only from a few localities. Southward no representative of this group is known on the coastal plain, and, if *C. limosus* had come from the south, traces of this migration might be expected. On the other hand, if it came from the north, as we here assume, the fact that it did not spread beyond Virginia may be accounted for by the presence of another group of this genus, the subgenus *Cambarus* (*blandingi*-section), in the southern parts of the coastal plain, which, like *C. limosus*, prefers ponds and sluggish streams. Indeed both species (*C. limosus* and *C. blandingi*) are found actually associated at the same localities (by Faxon, 1885*a*, p. 88, at Trenton, New Jersey, and by the writer in the Delaware and Raritan Canal at Princeton, New Jersey), but we must bear in mind that in New Jersey, and also in Maryland and Virginia, *C. blandingi* is an intruder, its chief domain being in the Carolinas.

The following are conclusions from the above considerations:

Cambarus limosus is an ancient species, characterized by morphological and geographical isolation. The most closely related forms are found in Kentucky and southern Indiana. An attempt to explain the presence of *C. limosus* at its present location has to connect its range with that of these related species. A connection by way of the Atlantic Coastal Plain southward is out of the question. Thus only the connection across the Appalachian system remains. The fact that the rivers just west of the mountains in western Pennsylvania are occupied by a more advanced group of species (*propinquus*-group) of a subgenus which is certainly of Preglacial age, as we shall see below, leads us to the conclusion that the *limosus*-group also must be not only Preglacial, but older than the *propinquus*-group. But at that time there was no direct way from the lower Ohio, where its center of distribution was situated, into western Pennsylvania and across the mountains, the Ohio having no existence as yet, and the general drainage in this region being to the north. This leads us to assume a former more northern range of the *limosus*-group, extending into Preglacial Canada; and this assumption furnishes an explanation why it was possible for the Glacial Epoch to cut the range of the *limosus*-group in two, leaving no representative of it in the region now drained by the middle and upper Ohio. *Cambarus limosus is a Tertiary type, and it reached its present area coming from the west and by way of the north, being driven south along the Atlantic Coastal Plain by the advancing ice of the Glacial Period. It survived during the Glacial Period in the region of the lower Delaware River and Chesapeake Bay, while* *all the rest of the former range of the group was covered by ice and its representatives were destroyed, with the exception of a small remnant in the southwestern portion of the range, in southern Indiana and Kentucky, outside of the glaciated area.* The reason why this group was destroyed in the glaciated area, and was not able to retreat southward and to survive in the intervening parts (Ohio, western Pennsylvania, and West Virginia), was that here the rivers were occupied by another group of the subgenus.

The above is a mere theory, and it remains doubtful by which way *C. limosus* reached the Atlantic Coastal Plain. The assumption that it was by way of the Erigan River and the St. Lawrence basin satisfactorily accounts for the facts, but this is the only point directly in favor it. However, the study of the distribution of *C. limosus* is not yet finished, since the actual boundaries of the distribution, chiefly to the north and south, are not positively known. But this does not concern us at present, since they are not situated in the State of Pennsylvania.

In *C. limosus* we have a species which survived during Glacial times in a part of the Atlantic Coastal Plain which is well to the north, not far from the southern edge of the ice. Of course this forms a part of Adams' (1902, p. 121) southeastern center in its widest sense, lying at its northeastern extremity. Although surviving not far from the edge of the ice, *C. limosus* cannot be considered as belonging to the *tundral biota* (Adams, 1905, p. 58), but it belongs very likely to the second wave (northeastern biota), with a slight suggestion of the third wave (southeastern biota) (*l. c.*, pp. 58 and 62). As Adams indicates, the first and second waves of Postglacial dispersion had their glacial homes in very narrow belts parallel to the southern edge of the ice, while the southeastern (and southwestern) biota covered in Glacial times wide tracts of country. The second wave largely invaded the coniferous forest-belt of Canada, while the third wave was more stable and did not spread so far northward. With regard to its geographical location during Glacial times, *C. limosus* should be classed with the *northeastern biota;* and with regard to its stability in Postglacial times, with the *southeastern.* But we are to consider that a Postglacial northward dispersion was rendered difficult in this case by the physiographical features of the country. The coastal plain with its sluggish streams and stagnant ponds disappears in northern New Jersey, the uplands (Piedmont Plateau) reaching the coast in the vicinity of New York Bay (see McGee, 1888, Pl. 2); this did not offer advantageous conditions for this species, and thus it remained within comparatively narrow limits in a corner, into which it was pushed in Glacial time. *C. limosus is a Tertiary relic* at the northern extremity of the coastal plain, which has not been able to expand its area to any considerable degree in Postglacial times.

2. *Cambarus propinquus, Cambarus propinquus sanborni and Cambarus obscurus.*

a. Summary of Facts. (See pp. 362–363; 368–369; 372–373.)

If we desire to arrive at a proper understanding of the distribution of *C. propinquus*, *C. propinquus sanborni*, and *C. obscurus*, they must be discussed together.

The area occupied by these three forms (see Pl. XLII, Fig. 3) includes eastern Iowa, southern Wisconsin, northern Illinois, Indiana, Michigan, Ohio, northeastern Kentucky, northern West Virginia, western Pennsylvania, western New York, and parts of Canada (Ontario and Quebec). In the western and northern part of this range *C. propinquus* is found; *C. propinquus sanborni* occupies the larger part of Ohio and parts of Kentucky and West Virginia; while *C. obscurus* has its chief domain in western Pennsylvania, passing southward into West Virginia and northward into New York. Thus it is apparent that the three forms occupy different sections of the general area of the group, *propinquus* being western (and northern), *sanborni* central, and *obscurus* eastern. As far as observations go all three forms are rather sharply separated geographically, although they come into contact at the edges of their ranges. This is especially true, as we have seen, in our state and the adjacent portions of Ohio and West Virginia, while in western Ohio and in Indiana nothing is known of the boundaries of the forms represented there.

In Pennsylvania only two of these forms are found (Pl. XLII, Fig. 2). *C. propinquus* is restricted to Lake Erie and its drainage; *C obscurus* belongs to the Ohio system, and is found everywhere in the western section of the state, in the Ohio, Monongahela, and Alleghany Rivers and their tributaries. The boundary toward the east is formed by the divide between the Alleghany and Susquehanna systems, and farther south generally by the Chestnut Ridge (with exceptions to be discussed below). Northward this species crosses over into the Genessee drainage, and extends into New York. It also crosses over into the Lake Erie drainage in Pennsylvania.

Along the western border of the state it passes beyond the state line into Ohio, the drainage belonging in the northern part to the Beaver River. Furthermore it goes down the Ohio and is found in all creeks running from Pennsylvania through the Panhandle of West Virginia as far south as Fish Creek in Greene County, Pennsylvania, and Marshall County, West Virginia. Fish Creek falls into the Ohio a little below Moundsville, West Virginia, and contains only the typical form of *C. obscurus*.

Going further down the Ohio conditions suddenly change. In Fishing Creek, Wetzel County, West Virginia, which empties into the Ohio near New Martinsville, about thirteen miles below the mouth of Fish Creek, *C. propinquus sanborni* appears. But the form here found is not typical. As we have seen above, it inclines somewhat toward *C. obscurus*, and one individual has been found which represents typical *C. obscurus*. In Middle Island Creek near St. Mary's, Pleasants County, West Virginia, which is about twenty-five miles further down the Ohio, the few specimens collected seem to be typical *C. propinquus sanborni*.

Thus it appears that *C. obscurus* goes down the Ohio River to about Moundsville, West Virginia. All the tributaries of the Ohio in the Panhandle possess this species, and very probably it will be found also in Ohio on the opposite side of the river. But crossing over the divide between this part of the Ohio and the Muskingum-Tuscarawas River in Ohio, we again find *C. propinquus sanborni* in the drainage of the latter. The western boundary of *C. obscurus* consequently is formed by the divide just mentioned, but this line crosses the Ohio River between Moundsville and New Martinsville, West Virginia (Pl. XLII, Fig. 2, and Pl. XLIII).

Further to the south in West Virginia in the drainage of the upper Monongahela this species has not been traced. It surely goes up the Monongahela beyond the southern boundary line of Pennsylvania, but how far has not been ascertained.

The fact that *C. obscurus* is found also in the Potomac drainage, in Wills Creek, between Hyndman, Bedford County, Pennsylvania, and Ellerslie, Alleghany County, Maryland, deserves special mention, and will be commented upon elsewhere.

b. Origin of the distribution of C. propinquus, propinquus sanborni, and C. obscurus.

In order to get a fair understanding of the distribution of these forms, we must take notice of the Preglacial physiography of the region in which they are found, for, as we shall see below, we are led to believe that these forms are of Preglacial age, and survived during the Glacial Period in the southern parts of the drainage systems, which now constitute that of the Ohio.

First of all, we should bear in mind that at the end of the Tertiary Period before the ice pressed down from the north, the Ohio River in its present form did not exist. In the whole region, drained now by the middle and upper Ohio, the drainage was at that time not to the west, but to the north, and it was collected by a river running in a northeasterly direction toward the present Gulf of St. Lawrence, (the Erigan River or Ancient Grand River).[47]

Disregarding some smaller streams, for instance the Old Middle and Old Upper Alleghany, which do not concern us here, three main rivers, tributary to the Erigan River, have been traced with more or less accuracy, and the evidence for their existence, although fragmentary, leaves no doubt as to the general correctness of the main features of this drainage, which differs so strikingly from that which exists to-day.

---

[47] This is the opinion of Spencer (1881 and 1894). Others believe that this river drained toward the Southwest, into the Mississippi; see Grabau, 1901, maps, p. 44 and 45 (Dundas River).

The easternmost of these rivers was the Spencer River, or Old Monongahela, or Old Upper Ohio,[48] which drained southwestern Pennsylvania, northern West Virginia, and a small part of eastern Ohio. West of it was the Old Kanawha River, or Old Middle Ohio, or Teays River (Leverett, 1902, p. 100, map, p. 101; Tight, 1903), which drained parts of West Virginia and Kentucky, and the larger part of central Ohio. The old Muskingum-Tuscarawas River belonged to this drainage, the Muskingum River not flowing southward, but westward and southwestward from near Zanesville, Ohio, to Circleville, Ohio, thus joining the Old Kanawha (Newark River; Tight, 1903, Pl. 1).

The divide of the Old Kanawha to the westward was formed by the Cincinnati uplift, and was situated according to Leverett (1902, p. 100) near Manchester, Ohio, on the present Ohio River. Beyond this divide we have the Lower Ohio system (Leverett, p. 109). The Preglacial lines of discharge in this region are rather obscure, but according to Leverett and Newsom (1902, p. 168, Pl. 6) it is probable that a large part of the present system of streams was tributary to the lower Ohio in Preglacial times, but that a small number of them may have had a northward discharge through the Great Miami basin in western Ohio (Leverett, p. 116). There are distinct indications of a northward drainage in the vicinity of Cincinnati (Cincinnati River, Tight, 1903, Pl. 1). This possibility is also admitted by Newsom (1902, p. 181).

We may take it for a well established fact that in Preglacial times at least two rivers existed in this region, the Spencer and the Old Kanawha, which did not drain into the Ohio and Mississippi in a southwestern direction, but flowed northward into the Erigan basin. Westward there was very likely a third river ("Old Miami") running in a similar direction; but in this region we arrive at the old Preglacial divide between the Lower Ohio and the Erigan River. It remains doubtful whether the latter drained to the St. Lawrence Gulf or to the Mississippi by the way of the present Wabash.

Assuming the theory of the former existence of an Old Miami (or Cincinnati) River, we see that there are certain interesting relations of these three old rivers to the present distribution of the three forms of *Cambarus* under discussion.

Of course, we must disregard those parts of the ranges of these forms which lie in the formerly glaciated area, for these are due to Postglacial expansion. But looking upon the localities south of the terminal moraine (Pl. XLII, Fig. 3) we see that only a few are known for C. *propinquus*, and these are all in southern Indiana (Brown, Monroe, and Green Counties),[49] and belong very likely to the old Lower Ohio drainage, but in the region where it comes into contact with the supposed Old Miami River (or possibly some other river flowing north in the State of Indiana). Since we have reason to believe (Ortmann, 1905*b*, p. 114) that the center of radiation of the subgenus *Faxonius*, to which the *propinquus*-group belongs, is in the central basin formed by the three great rivers (Missouri, Mississippi, and Ohio), *C. propinquus* distinctly points toward this center, of which southern Indiana forms part. This is the more interesting since we see that it is the most primitive species of the *propinquus*-group which most closely approaches the original center. In Preglacial times *C. propinquus* belonged to the northeastern extremity of the old Ohio drainage (Lower Ohio), and in this region there apparently was a chance for it to cross over the continental divide into the Atlantic (St. Lawrence) drainage. If, however, the Erigan River drained to the Mississippi, the presence of this species in the Lower Ohio and in the lower part of the Erigan River is more easily accounted for by direct communication of the waters.

---

[48] See above, p. 429. Descriptions are given by Foshay, 1890, White, 1893, and Leverett, 1902, p. 88 (with map on p. 89). Additional evidence has been furnished by Hice, 1903, p. 302. Another name is Pittsburgh River (Tight, 1903, Pl. 1).

Taking up the distribution of *C. propinquus sanborni*, we observe that until recently only one locality was known to the south of the drift, namely, the type locality in Carter County, Kentucky, which is undoubtedly in the drainage of the Old Kanawha River. In addition, I have discovered a number of localities in eastern Ohio (Carroll, Harrison, and Stark Counties), and in northern West Virginia, which belong to the same drainage (Newark River and Marietta River, tributaries of the Old Kanawha), which are also outside of the glaciated area (at Canton, Stark County, Ohio, close to the edge of the drift).

The chorological facts about the distribution of *C. propinquus* and *C. propinquus sanborni* are very meager, and not at all satisfactory; but as far as our present knowledge goes, all known localities of *C. propinquus sanborni*, outside of the drift, are in the drainage of the Old Kanawha, while none of the known localities of *C. propinquus* are in this drainage, but are situated to the west of it. Now, this mutual relation between distribution and Preglacial drainage becomes more evident when we look upon *C. obscurus*, the distribution of which I have studied more closely.

---

[49] They are close to the southern edge of the drift, and it is a little doubtful whether they are inside or outside of it. Disregarding the Illinoisan drift, they are surely outside of the Postillinoisan glaciation, as is also a locality in Franklin County, Ind.

Leverett (1902, p. 89, Fig. 1) has given a map of the Old Monongahela River, which is reproduced on Plate XLII, Fig. 1, and alongside of it, Plate XLII, Fig. 2, I give a map of the present distribution of *C. obscurus.* It is evident at a glance that there is close correlation between *C. obscurus* and this old river. The most important features are furnished by the western boundary. The divide between the section of the Ohio which runs along the Panhandle of West Virginia and the Muskingum-Tuscarawas drainage is the old divide between the drainages of the Spencer River and the Old Kanawha. This divide crosses the present Ohio just above New Martinsville (see Leverett's map, p. 90, Fig. 2: "probable early divide"). *As I have found* (p. 434) *this old divide coincides with the present boundary between C. obscurus and C. obscurus sanborni.* It also is significant that it is not the Tertiary (Preglacial) divide, which is located by Tight (1903, Pl. 11) just below New Martinsville, nor the "later divide" of Leverett (*l. c.*), but just the one which existed at the beginning of the Glacial Period. We shall have to return to this topic.

Thus it is clear, *first,* that the original separation of these two forms was brought about by the fact that they belonged to different river systems; *second,* that we must assume the Preglacial age of the *propinquus*-group; and *third,* that the distribution of these crawfishes furnishes additional evidence for the correctness of the view of the Old Monongahela and Old Kanawha, as held by Leverett (and others); and with reference to these crawfishes it seems to me that the following theory is rather well founded.

In Preglacial times, the propinquus-group, coming from the southwest (lower Ohio) reached the Erigan River drainage (either directly or by crossing a divide), of which it became characteristic.[50] It entered, consequently, also the southern tributaries of this river, and *owing to the fact that there were three main tributaries, this group developed the tendency to split up into as many geographical forms.* These were apparently the conditions when the Glacial Period began.

The chief effect of the advancing ice was that the northern parts of the range of this group were covered by ice. Only in the region of the headwaters of these rivers, to the south of the edge of the ice, was there a chance to survive, and survival here occurred. Both the Old Monongahela and the Old Kanawha were dammed up by the ice, and transformed into lakes (Lake Monongahela of White, 1896, and Lake Ohio, *cf.* Jillson, 1893, p. 19, and Map, Pl. 5, with the necessary restrictions), and this led to the result that the colonies of crawfishes belonging to the southern (upper) parts of these rivers became sharply separated from each other, and I think that the *tendency toward the formation of three species* (*C. propinquus, C. sanborni, C. obscurus*) *is directly due to this process and to physiographical conditions prevailing in the earlier part of the Glacial Period* (Kansan or Prekansan, *cf.* Hice, 1903, p. 300).

---

[50] We have seen that a similar dispersion very likely took place in the case of the *limosus*-group. The latter being more primitive, we must assume that it formed a first and earlier wave of immigration from the Lower Ohio into the Erigan drainage, while the *propinquus*-group came later. This movement is still going on. There is evidence of a subsequent Postglacial wave (later than the Postglacial migration of *C. propinquus*) also starting from the Lower Ohio, and represented by the *rusticus*-group, which again has all the morphological marks of a more recent type than the *propinquus*-group. But this is outside of the scope of the present paper.

Finally these lakes were connected and drained off toward the southwest, thus forming the present Ohio River (Postkansan, but before the Wisconsin stage, *cf.* Hice, 1903, p. 299); the areas of the three forms of crawfishes were reunited, but the different parts of the new Ohio drainage are occupied by different forms of the *propinquus*-group, remaining in their original areas; the upper Ohio is characterized by *C. obscurus*, the middle Ohio by *C. propinquus sanborni*, and the lower Ohio by *C. propinquus*.

But additional changes took place in Postglacial times. According to the present distribution these must have been greatest in the case of *C. propinquus*. Almost the entire range of this form lies within the glaciated area, and thus it is beyond question that its present distribution is largely due to the Postglacial migration northward and northeastward.[51] This migration possibly began at an earlier date than in the case of the other two forms. We know that in southern Indiana and southwestern Ohio an early retreat of the southern border of the ice took place, as is indicated by the presence of Illinoisan drift south of the early Wisconsin border (*cf.* Leverett, 1902, Pl. 2 and Pl. 11). There also was considerable recession of the ice of the Maumee-Miami glacial lobe in the earlier and later Wisconsin stage, while in central and eastern Ohio and western Pennsylvania (Scioto glacial lobe and Grant River glacial lobe) only in the later Wisconsin stage did recession take place (*cf.* Leverett, ibid., and Pl. 13 and Pl. 15). Toward the end of the later Wisconsin stage large lakes began to form in front of the receding ice, and this happened first in the western part of this region. The first lake thus formed was Lake Maumee (Leverett, p. 710 ff., Pl. 20 and 21), which had an outlet toward the west and southwest (Fort Wayne outlet; see also Grabau, 1901, p. 58). Lake Maumee was situated in northwestern Ohio, in the present Huron-Erie basin, and thus we see that the latter was opened first in its western part to an immigration from the southwest

---

[51] A loss of territory must have occurred in the south, *C. propinquus* losing ground in competition with *C. rusticus* which was pushing on from the south. This matter does not belong to our present investigation, but attention should be called to it.

(Indiana) at a time when this basin was entirely covered by ice further east, thus being closed more or less to an immigration from the central parts of Ohio (drainage of middle Ohio), and being closed entirely to an immigration from eastern Ohio and western Pennsylvania (drainage of upper Ohio).

This explains why *C. propinquus*, which survived in southern Indiana, had the first chance to spread northward and to enter the future Huron-Erie basin by way of Lake Maumee. The subsequent stages of this lake (Lake Whittlesey, Lake Warren, etc.), are all direct continuations in time of Lake Maumee, and so it is not astonishing that *C. propinquus*, after the final establishment of the St. Lawrence drainage,[52] is found all over this region, not only in the Lake Huron and Lake Erie basins, but also farther down, in Lake Ontario and the Lower St. Lawrence drainage. In the occupation of this whole region *C. propinquus* was not interfered with by the other forms, since no opportunity was given to *C. propinquus sanborni* and *C. obscurus*, to enter the Erie basin, the drainages of the middle and upper Ohio remaining permanently changed to the southwest, away from Lake Maumee, a condition which obtains, with very slight changes, up to the present time.

However, *C. propinquus sanborni* as well as *C. obscurus*, have entered the Lake Erie drainage. With regard to the first, it may be sufficient to state that it is found in Lorain County, Ohio, in rivers and creeks running into the lake, and this is apparently due to a comparatively recent immigration under similar conditions as in the case of *C. obscurus* in Pennsylvania. The latter species has been discovered by the writer in Crawford and Erie Counties, Pa., in streams flowing to Lake Erie, associated with the Lake Erie form, *C. propinquus*. Thus *C. obscurus* must have crossed the divide between the upper Beaver (Shenango) River and Alleghany River (French Creek) on the one side, and Lake Erie (Conneaut and Elk Creeks) on the other, and the question is by what means this was accomplished.

It is only natural that *C. obscurus*, surviving during Glacial times in southwestern Pennsylvania and West Virginia, migrated up the drainage of the upper Ohio, chiefly the Beaver and Alleghany Rivers, in Postglacial times, for after the end of the Glacial Period this system formed a unit[53], and no serious barriers to the dispersal were, or are, present. Thus it was easy for this species to go up toward the head-waters of these rivers and to closely approach the divide toward Lake Erie.[54]

---

[52] The change of the westward drainage to an eastward took place toward the end of the Glacial Period, as soon as the ice receded far enough to uncover Lake Ontario (Lake Iroquois), thus permitting the water to drain off through the Mohawk, and later through the St. Lawrence. This was accompanied probably by a depression of the land in the Northeast, culminating in the marine invasion of the St Lawrence valley (Champlain submergence). (See Grabau, 1901, p. 59 *et seq.*)

[53] As to the formation of the present Alleghany out of the former Lower, Middle, and Upper Alleghany, see Leverett, 1902, p. 129 *et seq.*

This would favor a direct crossing of the divide by actual migration over land, and indeed the river-species are able to survive when out of the water for a considerable time under certain circumstances, as I have ascertained by experiments. During hot and dry weather it is hardly possible to keep them alive for more than an hour or two; but in cool, cloudy, and damp weather I have found that specimens suspended on a string on an open veranda[55] were not dead after seven hours, and restored to water, recovered entirely. This might at least render a migration over land possible, but I do not think that it actually takes place, since it has never been observed, either by others or by myself, that *C. obscurus*, or any other species classed ecologically with the river-species, leaves the water voluntarily. On the other hand it is possible that *C. obscurus* may undergo a passive transport from one drainage to the other, as for instance by birds. However, I do not believe that the crossing of the divide toward Lake Erie is due to the latter cause. It seems to me highly improbable, not that birds should be able to carry crawfishes for a long distance, but that it should happen that a bird should take up a crawfish in one stream, carrying it to another safe and sound, and drop it there without hurting it. Birds do take crawfishes[56] and sometimes carry them short distances, but this always results in serious injury, even if the specimen is not immediately eaten. Thus, even though we may admit that crawfishes might be transported by birds without being injured, such cases must necessarily be extremely rare, and do not happen often enough to effect the establishment of a species in a drainage system from which it was originally absent.

There are other considerations which make the assumption of passive transfer improbable in our case. Toward the east *C. obscurus* is (with exceptions to be discussed below) rigidly restricted to the Ohio drainage, and nowhere crosses into that of the Susquehanna. If transport were at all probable we should expect to find that it had taken place here, as well as in the region of Lake Erie.

---

[54] At Linesville, Crawford County, I found this species in the very headwaters, almost in the springs running into Shenango River just south of Summit, which is on the divide.

[55] Particulars of one of the experiments (I have made a series) are as follows: November 9, 1905. Cloudy day. Mean temperature: 31° F. Light breeze from West-South-West, and light snow in afternoon. Specimens of *C. obscurus* suspended on strings on veranda with southern exposure. Beginning of experiment 9 a. m. One specimen taken in at 2 p. m., another taken in at 4 p. m., and put into water. Both alive and vigorous next morning, and were kept alive till December 18, when they were thrown into alcohol.

In midsummer, on hot days, I often observed that the vitality of *C. obscurus* becomes very low after they are only a short time out of water. They may die within an hour, without having been subject to any other injury than that caused by the removal from the water.

[56] Mr. W. E. C. Todd informs me that remnants of crawfish are quite usual in the nest of the kingfisher. I have seen, in the collection of the Department of Agriculture, Harrisburg, a specimen of *C. bartoni*, taken from the stomach of a kingfisher.

Further, and this is the most important objection to the transport theory, while *C. obscurus* has invaded the Lake drainage, not only in Pennsylvania, but also in New York (Genessee River), in no case has the opposite taken place namely, that *C. propinquus* has invaded the Ohio drainage. If the crossing of the divide were due to passive transport, the same cause should have acted in both directions; but *C. propinquus* is entirely absent from the Ohio system.

The latter objection holds good also with reference to another assumption, that *C. obscurus* may have crossed into the lake drainage by the aid of the old canal which connected the Beaver River with Lake Erie (Erie extension of Beaver canal). This canal (see Jenkins, 1903, p. 288, 289) was in part used as early as 1834, and was completed in 1844; it was abandoned in 1871, and it cannot be denied that by it *C. obscurus* might have been able to reach the Erie drainage. I would not hesitate to accept this as correct if it were not for the fact that *C. propinquus* has not gone in the opposite direction.[56a] Precisely in the region of this old canal my collections are very complete, and are supplemented by those of others (Messrs. O. E. Jennings, D. C. Hughes, and W. R. McConnell), so that I am positive about the absence of *C. propinquus*.

On the other hand, we have seen that the specimens of *C. obscurus* from the tributaries of the lake seem to approach more closely those of Beaver River than those of French Creek. This would be in favor of the canal-theory, the canal running from Newcastle by the way of Shenango River to Conneaut Creek (Jenkins, *l. c.*), while French Creek was not so closely connected with it (although there was a "French Creek feeder"). The absence of *C. propinquus* in the Beaver drainage may be due to the fact that in Erie County, the canal was not so closely connected with the streams running to the lake, and that thus the lake species could not get into the canal; or else *C. propinquus* being the weaker species of the two could not make any headway against the more vigorous *C. obscurus*.

There remains another theory, namely, that the migration of *C. obscurus* into Conneaut and Elk Creeks is due to stream-piracy. The latter has undoubtedly taken place in this region in Postglacial times. The Postglacial divide between Lake Erie and the Ohio was formed originally by moraines of the late Wisconsin stage (Lake escarpment morainic system. See Leverett, 1902, Pl. 18; also Carll, 1880, Pl. 1) or by higher elevated parts of the non-morainic drift lying immediately in front of this morainic system. The fall of the creeks running northward to Lake Erie from this divide is much more considerable than that of those running southward, and thus it is clear that erosion on the northern slope must have been more efficient than on the other side. The consequence is that the tributaries of Lake Erie, at least some of them, have worked back through the original divide, and have captured parts of the original Postglacial drainage of the Ohio. This is most evident (see Pl. XLIII) in the cases of Conneaut and Elk Creeks, and it is just in these creeks that I found *C. obscurus* associated with *C. propinquus*,[57] while in Walnut Creek, which has apparently not entirely cut through the original divide, *C. obscurus* is not found.

[56a] It should, however, be borne in mind that the discharge of the water from the canal was downward toward the lake and thus that migration might in that direction have been easier than in the opposite. — EDITOR.

Thus it is possible that the presence of *C. obscurus* in the Lake Erie drainage is due to stream-piracy. Both species, *C. obscurus* and *propinquus*, are associated here, but it seems that they are antagonistic to each other to a certain degree. In the tributaries of Conneaut Creek I found *C. propinquus* exclusively, while Conneaut Creek itself contained both, but *C. obscurus* prevailed, and it appears as if the latter had driven out the other species, which took refuge in the smaller tributaries.

We might expect to obtain some light upon the question, whether *C. obscurus* reached the Lake Erie drainage in consequence of stream-piracy or by the help of the canal, by the analogy offered in the Genessee drainage, but conditions seem to have been not entirely identical here. The type locality of *C. obscurus* (see Pl. XLII, Fig. 3) is the Genessee River at Rochester, Monroe County, New York, where this species also is found associated with *C. propinquus*. Mr. W. P. McConnell has discovered *C. obscurus* in the upper Genessee drainage near Ulysses, Potter County, Pennsylvania. The material consists of numerous males of the first and second form and of females, and there is not the slightest question that this is the true *C. obscurus*, no trace of *C. propinquus* being present here. How did this species get from the Alleghany drainage into that of the Genessee?

The drainage of the Genessee River lying entirely within the glaciated area, this must have happened in Postglacial times. Fairchild (1896, p. 423) has shown that during the recession of the ice the Genessee basin was occupied by a lake, which had its outlets in different directions successively, draining either to the Susquehanna or to the Ohio. He distinguishes ten stages, and the sixth was the last in which the water flowed to the Susquehanna; in the seventh and eighth stages Genessee Lake became connected with Lake Warren, which drained to the west into the Mississippi basin (but not into the upper Ohio), and finally the St. Lawrence drainage was established. Thus we see that in the beginning Genessee Lake was connected repeatedly with the upper Ohio (Alleghany River) drainage, but it is not probable that *C. obscurus* immigrated at this time, for then it ought also to have reached the Susquehanna drainage, since the lake discharged its water into the Susquehanna (through the "Burns outlet") subsequently to the last connection ("Cuba outlet") with the Alleghany River. (See Fairchild, 1896, map, Pl. 19.)

---

[57] The sources of Elk Creek are in a tamarack-swamp, which also drains to the south, to French Creek, so that some kind of a direct connection may be present. I have not visited this swamp.

After this a discharge toward the upper Ohio was never re-established. But we know that stream-piracy has taken place in this region (headwaters of the Genessee), and although in some cases the Alleghany River seems to have captured parts of the Genessee drainage (Oil Creek has captured the head of Black Creek; see Leverett, 1902, p. 207), the opposite has positively also taken place, for instance, Knight Creek and Van Campen Creek have captured, according to Fairchild, small lakes that once discharged towards Oswayo Creek, a tributary of the Alleghany. This may have happened after the sixth stage of Lake Genessee, when there was no longer any connection with the Susquehanna system, and would explain the presence of *C. obscurus* in the Genessee River and its absence in the Susquehanna.

The eastern boundary of *C. obscurus* in Pennsylvania is formed, generally speaking, by the divide between the Ohio drainage in the west and that of the Susquehanna and the Potomac in the east. This is most evident in the northern part of this line, in Potter, McKean, Elk, Clearfield, Jefferson, and Indiana Counties. This species goes up the Alleghany River probably into Potter County, for it has been found not far away from the county line at Larabee, McKean County. It has not been found in the drainage of Clarion River in Elk and Jefferson Counties, but this is very likely due to the excessive pollution of this river. There is hardly a watercourse known to me in Pennsylvania which is in a worse condition than Clarion River in Elk County. The wood-pulp mills at Johnsonburg, the tanneries at Ridgway, the chemical factory at St. Mary's discharge refuse into it, and Toby Creek adds sulphur water from the mines above Brockwayville (Jefferson County). Similar conditions prevail in Red Bank and Sandy Lick Creeks in Jefferson County, but I have been able to ascertain the presence of this species near the head of Sandy Lick Creek at Dubois, Clearfield County (about 10 miles from the divide).[58] In southern Jefferson County, *C. obscurus* is not present in Mahoning Creek at Punxsutawney (although *C. bartoni* was there), this creek being slightly polluted by mine-waters; but I found it here in a pond connected with the creek. In Indiana County it is present in all creeks running to the Alleghany and Conemaugh (Little

---

[58] I found this species here on June 16, 1905. Only two living specimens were taken, but numerous dead ones were lying in the creek. Apparently some injurious substance had been quite recently introduced into the water.

Mahoning Creek, Crooked Creek, Two Lick, and Yellow Creeks). Crossing over the divide in this region into the drainage of the West Branch of the Susquehanna, no trace of this species is found. I hunted for it in vain in Sinnamahoning Creek in Cameron County, in the West Branch and its tributaries in Clearfield, Cambria, and Indiana County (near Cherry Tree), and in Clearfield Creek in Cambria County.

In this whole region (headwaters of the West Branch) stream-piracy has taken-place on a large scale, the whole basin of this river having been taken away from the original Alleghany drainage. But *C. obscurus* has not been taken over. According to Davis (1889, p. 248, see also above, p. 430) this stream-piracy fell largely into Pretertiary times, and although we are to assume that it continued during subsequent times (p. 430), it must have been rather slow, and insignificant, chiefly so in Glacial and Postglacial times, which alone are to be considered in the case of *C. obscurus.* Although this species was present in the Alleghany River drainage, it did not go up into the headwaters, remaining away from the actual divide for a distance of about ten to twenty miles. Under these circumstances, as stream-piracy was only going on at the headwaters, no good opportunity was offered for this species to cross the divide.

In Cambria County the continental divide bends to the east, and is transferred to the main chain of the Alleghanies (Alleghany Front); but the eastern boundary of *C. obscurus* does not follow it. Here it is the Chestnut Ridge which constitutes the boundary, beginning in southern Indiana County, and continuing through Westmoreland and Fayette Counties to the southern state-line. Generally *C. obscurus* does not pass beyond this ridge into the higher parts of the Alleghany Plateau, but there are two exceptions. It is found in the Loyalhanna River in the Ligonier valley, and in Indian Creek, and in this region it is not the Chestnut Ridge, but the Laurel Hill Ridge which forms the eastern boundary. In the Conemaugh River and the Youghiogheny, this species has not been able to pass upstream beyond the Chestnut Ridge, since both rivers become very rough above this point, and this roughness apparently existed also at the end of the Tertiary Period, when the rivers descended, through the Chestnut Ridge, from the elevated Old Tertiary peneplain to the late Tertiary base-level, at which they were then flowing.[59]

---

[59] According to Campbell (1903, p. 292) the peneplain of southwestern Pennsylvania, elevation 1200 to 1300 feet, is identical with the Old Tertiary Harrisburg peneplain; and according to White (1896, p. 377), the Old Monongahela (with the Youghiogheny) of Late Tertiary age was about at base-level. Stevenson (1878, p. 259) has called attention to an old terrace of the Youghiogheny at Connellsville, which apparently corresponds to the late Tertiary base-level, 200 feet above the present level (894 feet) at about 1100 feet above the sea. At Confluence it is 1820 feet high, thus giving to the river between Confluence and Connellsville a fall of about 700 feet at the end of the Tertiary. At present the fall of the river is only 432 feet between the points named. Although the identity of the old terraces is not demonstrated, the difference of elevation is so great that a considerable fall of the Tertiary river is beyond doubt, and thus at that time a barrier to the upstream dispersal of *C. obscurus* must have existed here.

As has been repeatedly mentioned, *C. obscurus* has been discovered in Wills Creek, a stream which belongs to the Potomac drainage, at Hyndman, Bedford County, Pennsylvania, and Ellerslie, Maryland. This locality is entirely isolated and about 40 to 50 miles distant from the nearest parts of the main range in Westmoreland and Fayette Counties, separated from the latter by that part of the Alleghany Plateau which is included between Chestnut Ridge, Laurel Hill Ridge, and the Alleghany Front. In this region, chiefly in the drainage of the upper Youghiogheny and Castleman Rivers, *C. obscurus* is missing, of which fact I am quite positive, having searched for it in vain at the following localities: the Youghiogheny River at Ohiopyle, Fayette County, same river and Laurel Hill Run, Confluence, Somerset County; Youghiogheny River, Selbysport, Garrett County, Maryland; Castleman River, Rockwood, Somerset County; Flaugherty Creek, between Meyersdale and Keystone, Somerset County.

Under such conditions stream-piracy is out of the question. For some time I suspected that *C. obscurus* might be present in other parts of the upper Potomac drainage, but this is not the case. I have investigated the Potomac River at Cumberland, Maryland, and above Cumberland (Rawlings, Alleghany County, Maryland), and further up, where it forms the boundary between Garrett County, Maryland, and Mineral and Grant Counties, West Virginia; but I have not seen a trace of this or any other river-species. Below Cumberland *C. limosus* turns up. Thus the presence of *C. obscurus* in Wills Creek is very local, and restricted to only a small part of the creek. I found it at Ellerslie, Maryland, but not below this point, although I investigated the whole creek from Mt. Savage Junction to the Pennsylvania state-line. At Hyndman it is quite abundant, but only below a point about half-a-mile south of the railroad station, thus occupying only about eight or nine miles of the creek.

These facts are rather strange, and, I believe, can only be explained by the assumption of artificial introduction by human agency. I do not think that it was necessarily intentional, but it may be due to accidental stocking of the creek with this species, which is not altogether improbable, if we consider that in this region a good deal of fishing is done, and that fishermen from places between Pittsburgh and Connellsville go over this whole region, and frequently use crawfishes as bait, capturing them in one part of the country, and carrying them for their purposes to other parts. If *C. obscurus* has not been transported in this way to Wills Creek, intentionally or accidentally, I have no other explanation to offer.

The above theory as to the origin of the distribution of the group of *C. propinquus* explains the facts, as far as I can see. Our knowledge of the distribution of

C. propinquus and of *C. propinquus sanborni* is rather unsatisfactory, but none of the known facts is opposed to our theory. With reference to *C. obscurus* in Pennsylvania, I think our assumptions are well supported. *Cambarus obscurus is a Preglacial form, belonging to the Old Monongahela (or Spencer) River, which survived during Glacial times in the headwaters of this river (Lake Monongahela), and spread out, in Postglacial times, over the whole of the Upper Ohio drainage (in addition to the Ohio and Monongahela, over the drainages of the Beaver and the Alleghany Rivers), and was only checked in its dispersal in the direction toward the mountains by the roughness of the streams.* The Ohio River of Postglacial times opened a way down stream, but *C. obscurus* was unable to spread in this direction, since these parts were occupied by another closely allied species, *C. propinquus sanborni.* It has slightly entered upon the territory of the latter (Fishing Creek), but has not been able to crowd it out or to conquer it. Similar conditions prevail in the Lake Erie drainage, which has been reached in consequence of stream-piracy, or else, by the help of modern canals. Here it came into contact with *C. propinquus.* In both cases (in West Virginia and Erie County, Pennsylvania) we see that the other species show indications of an inclination toward *C. obscurus.* I believe we have to deal here with *hybridization*, but this will be discussed later. Finally the species has crossed over into the Lake Ontario drainage in the region of the headwaters of Genessee River, presumably in consequence of stream-piracy. In the upper part of this system, in Pennsylvania, it did not find any competition, and is alone represented there, while in the lower part, at Rochester, N. Y., it is again found associated with *C. propinquus.* Further details with respect to these parts are not at hand.

Comparing the distribution of the *propinquus*-group with Adams' scheme of Postglacial dispersal of the biota of North America, we see at a glance that the whole group belongs to his *northeastern biota* of the *second wave* (Adams, 1905, p. 58). The biotic preserve of this element, during glacial times, was not far from the southern edge of the ice, in what is now the Ohio drainage, but it was restricted to this western part, and was not extended east of the Alleghany Mountains. In Postglacial times this group advanced northward, forming part of the second wave, which is most clearly seen in the present distribution of *C. propinquus*, which largely entered the coniferous forest-belt in Michigan, New York, and Canada. The other two forms (*C. propinquus sanborni* and *C. obscurus*) did not take much part in the migration of this wave, since they found a barrier to the north in the shape of the continental divide, and then, after they had crossed this divide at certain points, they found competition in *C. propinquus*, which had populated the whole St. Lawrence drainage at an earlier date ("biocenotic barrier"). In New York state, however, *C. obscurus* has advanced north in the Genessee basin to a considerable distance.

3. *Cambarus bartoni.*

a. Summary of Facts. (See pp. 381–386.)

Cambarus bartoni is very uniformly distributed all over the state, being, however, rather scarce in the extreme northwest in Erie County, where it is replaced by the form *C. bartoni robustus.* We shall discuss this later.

The species extends considerably beyond the limits of this state, chiefly toward the southwest and northeast. In these directions it ranges from Tennessee and North Carolina to New Brunswick and Quebec. Westward it reaches central Kentucky and southern Indiana. The Atlantic Coastal Plain is apparently not invaded by it to any considerable degree.

We clearly see that its range follows the main strike of the Appalachian system, and knowing that ecologically this species is a form of the rapid and cool waters of the uplands and mountains, living preferably in small streams and even springs, we understand that the distribution must be entirely different from what we have learned with reference to the river-species already discussed.

In Pennsylvania conditions seem to be favorable for this species everywhere, possibly with the exception of a very narrow strip on the eastern border, along the Delaware River (coastal plain); but even here it approaches the lowlands very closely, the Piedmont Plateau reaching the river at many places.

In the mountains elevation is no barrier for it, I found it myself at 2,600 feet on Laurel Hill Ridge, west of Jennerstown, and at 2,300 feet near Sandpatch, Somerset County, and at other places at elevations not much less (Chestnut Ridge in Westmoreland County; near Cresson, Cambria County; Keating Summit, Potter County). At Davis, Tucker County, West Virginia, I collected it in Blackwater River at 3,050 feet, and Faxon, 1898, p. 649, records it from Roan Mountain, North Carolina, 6,000 feet.

b. Origin of the distribution of C. bartoni.

The first point is to ascertain the center of radiation of this species. As I have pointed out in a previous paper (1905, p. 121), we must regard the southern section of the Appalachian system as the original home of the subgenus *Bartonius*, to which this species belongs, and (*l. c.*, p. 122) the advance and dispersal of the subgenus took place over the eastern mountains of the United States, the axis of the dispersal being directed from southwest to northeast.

We have reason to believe that the origin of this species falls into Preglacial times, it being rather primitive within the subgenus (at least in comparison with the *diogenes*-group). If this is the case it very likely extended in the Tertiary at least as far north as at present, but the advancing ice of the Glacial Period must have driven it south again, and it must have survived in the mountains of Virginia, West Virginia, and states further south. Possibly southern Pennsylvania formed part of its preserve in Glacial times, for the peculiar preference of this species for cold water admits this assumption. Be this as it may, it is certain that after the retreat of the ice this species advanced, occupying or reoccupying the whole state of Pennsylvania, and keeping on in its northward migration, until finally reaching its present range.

This advance in a northeastern direction clearly agrees with Adams' *third highway of dispersal* (1902, p. 123) along the Appalachian chain, and *C. bartoni* also belongs to the *northeastern biota* of the *second Postglacial wave* (1905, p. 58). What is interesting in this case is that an aquatic creature follows here the main strike of the mountains, independent of the drainage systems. I have previously called attention to this fact (1905*b*, p. 129), and have pointed out that this is rather the rule with the subgenus *Bartonius* (this has been observed already by Faxon, 1885*a*, p. 179). There is not the slightest doubt that this peculiarity is connected with the ecological laws governing this species. It lives generally in the region of the headwaters of the streams, where the dendritic conformation of the drainage systems and their mutual interlocking favors frequent shifting of the divides in consequence of stream-piracy.

Moreover, *C. bartoni* is a form which habitually leaves the water. It is found not only in small streams, but also in springs, often at places where there is a very scanty supply of water, and this has forced it to often assume burrowing habits. Like *C. obscurus* it is able to survive exposure to the open air for a considerable time, provided the temperature is not too high, and thus it is easy to imagine that it may cross over divides during rainy or cloudy weather, wandering from spring to spring in the mountains. On the other hand, we see that *C. bartoni* is not entirely absent from larger streams, and if once established in a small part of the drainage of a certain river it may easily be distributed over the rest of it by simply following the course of the stream. Thus it is not strange that this species has occupied the whole of the state, and this uniformity of distribution is chiefly due to the fact that the whole of Pennsylvania is hilly or mountainous, offering everywhere favorable conditions for this species. The general dispersal is due to two causes: first the ability of this species to cross watersheds by active migration; and second to stream-piracy, which has apparently played a considerable part in its dispersal.

It should be noted, as we have seen above, that the size of this species decreases markedly in the eastern section of the state. This fact is significant, in so far as it points out that the center of radiation for the state of Pennsylvania is rather on the western side of the mountains than on the eastern (see Adams, 1902, p. 122, "*fourth criterion for the determination of centers of dispersal*").

4. *Cambarus bartoni robustus.*

a. Summary of Facts. (See pp. 390–391.)

This form is found in Pennsylvania in a rather continuous area in the extreme northwest, in McKean, Warren, Erie, and Crawford Counties, both in the Alleghany River and the Lake Erie drainages. It is often associated with the typical *C. bartoni*, but has been found at different localities in Erie County without the latter. In addition it is not rare in the northeastern part of Allegheny County in the Alleghany River, and its tributaries, and has also been found in Chartiers Creek, in southwestern Allegheny County. Here it is always associated with the typical form.

In no other part of the state has this variety been discovered, and it is very important to note that no trace of it has been found in southwestern, central, southern, and eastern Pennsylvania. Although *C. bartoni* is abundant in these parts, and particular attention has been paid to the possible presence of *C. bartoni robustus*, all attempts to find it have failed, and I feel justified in asserting that it is absent here.

I am not so sure of this with reference to the region between Crawford and Warren Counties on the one side, and Allegheny County on the other. I have searched in this section for *C. bartoni robustus*, for instance near Tionesta, Forest County, at Oil City, Venango County, in Mercer and northern and central Butler Counties, and near Kittanning and Mosgrove, Armstrong County, but did not discover it. However, it is possible that it is present along the course of the Alleghany River, in the river itself, and some of its tributaries, in Forest, Venango, and Armstrong Counties. In some of the places mentioned I did not strike streams which looked very favorable, being generally not large enough. Yet in Erie and Crawford Counties I sometimes found this species in rather small streams. Conditions in Otter Creek, Mercer County, Slippery Rock Creek and Thorn Creek, Butler County, were apparently identical with those under which it is generally found in Erie County, but this form was not found.

b. Origin of the distribution of C. bartoni robustus.

Considering that the true *C. bartoni robustus* is a northern form, being found outside of Pennsylvania in northern Ohio, western New York, and Canada (St. Lawrence Basin), its center of distribution seems to be at the northwestern edge of the range of *C. bartoni*, in the St. Lawrence drainage. In Pennsylvania, however, it has crossed the continental divide, and has invaded the Alleghany River drainage in McKean, Warren, and Crawford Counties, and possibly has come down the Alleghany River as far as Allegheny County, spreading into some of its smaller tributaries.[60] This assumption seems plausible if we take into consideration only the Pennsylvanian material and that from the St. Lawrence Basin. We would have here a case of distribution which is entirely unique. *C. bartoni robustus* should then be regarded as a Postglacial form, which originated in the St. Lawrence drainage, and in Pennsylvania spread southward, coming from the north.

But there are objections to this view. *C. bartoni robustus* has been reported also from Virginia, Maryland, and Kentucky, and this, of course, would not be in favor of this theory. However, as has been said above (p. 392), I am inclined to believe that this southern form is not the same as the northern. If this view should be correct, I should regard *C. robustus* as a good species, and then the above opinion would hold good.

But further, the morphological characters of *C. bartoni robustus*, as compared with those of the typical *bartoni*, are distinctly more primitive. The shape of the rostrum is decidedly more archaic, the original form of the rostrum in the subgenus *Bartonius* being rather elongate, and not short and broad as in *C. bartoni*. The frequent presence of distinct lateral spines on the carapace is undoubtedly a primitive character; and the ecological peculiarity of preferring larger streams than are haunted by the typical form might also be regarded as a remnant of more primitive conditions. This, of course, would be strange in a Postglacial form, originating within the glaciated area, and we rather ought to expect a higher differentiation than the original, typical form.

Until the question of the identity of our northern *C. bartoni robustus* with the southern form, which bears the same name, is settled, we cannot form a final opinion. If both forms should be actually identical, we might have to deal with two races of *C. bartoni*, an older one (*C. bartoni robustus*), which possibly constituted a first wave of migration from southwest to northeast, which was overrun and crowded out by a later wave, consisting of *C. bartoni typicus*. Remnants of the older stock have been able to survive only at a few, scattered localities in the south, while in the northwest a more continuous and solid colony has remained. The scarcity or even absence of the typical *bartoni* in Erie County, Pa., which in our state is the chief domain of *C. bartoni robustus*, would support this view. *C. bartoni* has not yet invaded this region to such a degree as to crowd out the other form. Though I must confess that it does not strike me as very likely that the smaller form should be able to conquer the larger one.

---

[60] The Alleghany River, between Sandy Creek and Verona, has been investigated repeatedly. It is a curious fact that Dr. D. A. Atkinson collected here a large number of *C. obscurus* on September 17, 1900, but not a single *robustus*. I was at the same place on June 1, 1904, together with Dr. Atkinson and Dr. O. T. Cruikshank, but we did not collect this form (conditions were unfavorable); on November 19, 1904, I spent a whole day there, collecting numerous *C. obscurus*, and a few *C. bartoni* (typical), but not a single *robustus* was seen. When I visited this place again, on September 7, 1905, I secured within a short time six specimens of *C. bartoni robustus*, and on September 30, 1905, I found three fine specimens a little further up the river, at Hulton, although I did not hunt very diligently. Is it possible that the migration of this form down the river is going on? Does it gradually become more abundant?

Further investigations on this question should be made outside of this state.

5. *Cambarus carolinus.*

a. Summary of Facts. (See pp. 396–397.)

This species (see Pl. XLIII) is found in Pennsylvania in the southern part of the Alleghany Plateau, between the Chestnut Ridge in the west, and the Alleghany Front in the east, preferring the high valleys in this region, but not going up to the highest elevations of the mountains. Thus, although abundant near Meyersdale in Somerset County, it does not go up the valley of Flaugherty Creek toward Sandpatch. I have searched for it in vain between Meyersdale and Keystone, and at Sandpatch. In a northern direction this species ranges in the valley between the Chestnut Ridge and the Laurel Hill Ridge as far as southern Westmoreland County. Here the northern boundary is formed by the cross-divide in this valley separating the headwaters of Indian Creek from the Ligonier Valley. I am quite positive of this boundary, since I have searched in vain for chimney-builders all over Ligonier Valley from Idlepark (below Ligonier) to the sources of the Loyalhanna River. Coming across the divide to Jones' Mills, within a short time I discovered this species. In the longitudinal valley between the Laurel Hill Ridge and the Alleghany Front, this species has advanced further north. It has crossed the divide between the Castleman River drainage and that of Stony Creek (tributary to the Conemaugh), and I found it near Listie and Windber, in Somerset County. At the latter place it seems to attain its northern boundary. At all events I failed to find it near Lovett in Cambria County, in the high valley of Laurel Run, which to all appearance affords congenial conditions for its presence being rather swampy in many places. I have also searched for it unsuccessfully in the region of Cresson, Cambria County, and at several places further north.

The rest of the range of this species is entirely to the south of this state, in Maryland, West Virginia, Virginia, North and South Carolina (disregarding the isolated report from the Indian Territory, in which I do not put much faith). No particulars are known about its boundaries, but in this region also it is restricted to the mountains.

b. Origin of the distribution of C. carolinus.

Generally, conforming to the subgenus *Bartonius*, the center of radiation of this species is to be sought in the southern part of the Appalachian system. It has followed in its migration the strike of the mountains, keeping to the higher parts of the latter. Thus it has entered southern Pennsylvania, being restricted here to the highest portions of the Allegheny Plateau.

The lowest elevation at which I found it is at Ohiopyle, Fayette County, 1,250 feet, and at Dunbar, Fayette County, 1,260 feet. (At the latter place a few stragglers — two specimens — were taken as low as 1,070 feet, associated with *C. diogenes*, but here they had apparently come down from the top of the mountain, where this species was abundant at 1,260 feet.) All other localities in Pennsylvania were higher, generally between 1,500 and 2,000 feet.

The northern boundary of this species in our state is formed by two different, opposite features in the physical geography. Between Chestnut and Laurel Hill Ridges it is a cross divide of the longitudinal valley; between Laurel Hill and the Alleghany Front the deep erosion of the original longitudinal valley by the headwaters of the Conemaugh River forms the boundary. We do not know much of the geological history of this region, but it seems to me that the floors of these high valleys with their extensive clay deposits form a part of a former base-level, namely, that of the Old Tertiary peneplain identified with the Harrisburg peneplain by Campbell (1903, p. 293). In northern Somerset and southern Cambria Counties this has been eroded by the Conemaugh system, thus removing a good deal of the clay bottoms, which seem to be an essential condition for this species, and consequently the lack of this feature, or its interruption by the Conemaugh system at the northern end of Somerset County, has formed here the barrier to the dispersal of *C. carolinus*.

To all appearances *C. carolinus* is a Postglacial immigrant into this state. The northern boundaries in both of the longitudinal valleys are rather insignificant, and we should expect that *C. carolinus*, being a chimney-builder and able to leave the water for a considerable time, should be able, like *C. bartoni*, to cross boundaries of this character. We should even expect that it would be better fitted to do so than *C. bartoni*. In fact *C. carolinus* must have done so repeatedly on its way from the South, being found in the upper drainages of rivers running in different directions, for instance, the upper Youghiogheny in Maryland, the upper Potomac in Maryland and West Virginia, upper Decker's Creek (tributary of the Monongahela), and upper Cheat River in West Virginia.[61] That it has been checked in Pennsylvania by such minor barriers as an insignificant divide and a deeply eroded system of valleys, renders it very probable that these obstructions are only temporary, and may be overcome in time, and, on the other hand, that the immigration of this species is rather recent, its northward migration being not yet finished, but only temporarily stopped.

---

[61] As to stream adjustments and migration of divides in Garrett County, Maryland, See Abbe, 1902, p. 47, 53.

The fact that this species is restricted to a narrow strip within the mountains is clearly due to its ecological habits. It prefers a certain altitude and clay bottoms. The latter are found in Pennsylvania chiefly on the Old Tertiary base-level, and this is represented to a large degree only within the mountains. East of the Alleghany Front and west of the Chestnut Ridge only insignificant remnants of this base-level are found, and thus this species is missing.

We do not know anything about the Preglacial history of this species, and the facts at hand furnish no evidence with regard to this question. According to the morphological characters, and compared with *C. diogenes* and *C. monongalensis*, we must assume Preglacial age for it. Its immigration into Pennsylvania probably is Postglacial, and thus it possibly belongs to Adams' *third wave* of migration, starting from the *southeastern* center (Adams, 1905, p. 62). However, in analogy to *C. monongalensis* it may belong to the *second wave*, and the *northeastern biota* (see below under *C. monongalensis*).

6. *Cambarus monongalensis.*

a. Summary of Facts. (See pp. 400–401.)

Cambarus monongalensis occupies in Pennsylvania (see Pl. XLIII) a continuous area in the southwestern part of the state. Toward the east, beginning at the southern state-line, the limit of the distribution is formed by the Chestnut Ridge as far as the point where the Loyalhanna River cuts through this ridge in Westmoreland County. From this point the boundary follows the Loyalhanna to the north, and continues northwestward along the Kiskiminetas River. From the point where the Kiskiminetas empties into the Alleghany, the latter river, and further down the Ohio, form the northern boundary of this species, until the Ohio leaves the state in Beaver County.

Within this area this species has been found wherever it has been searched for, namely: in Greene, Washington, and southern Beaver Counties; in the northwestern section of Fayette County; in the larger part of Westmoreland County, and in southern Allegheny County. It has also been traced beyond the boundaries of the state in a western and southern direction: it is found all over the Panhandle of West Virginia (Hancock, Brooke, Ohio, and Marshall Counties), and has also been found at Morgantown, Monongalia County. It undoubtedly goes further south in West Virginia, but no records are at hand from these parts.

The writer was unable to discover this species in the state of Ohio (Harrison, Carroll, and Stark Counties), and its absence north of the Ohio-Alleghany River is well established (with one exception to be presently mentioned). Particular pains have been taken to ascertain the latter fact. While it is very abundant in Allegheny County, south of the Alleghany and Ohio Rivers, the writer has not in a single instance found it north of them. He has searched in vain at many localities in northern Beaver, northern Allegheny, in Armstrong, and Butler Counties, and further north. At one single locality, however, on the northern side of the Alleghany River it is present. It was found by Dr. D. A. Atkinson near Squaw Run, at Aspinwall, Allegheny County (more correctly near Claremont). This seems to be a very restricted locality. The writer did not visit it himself, but he hunted all over the region around it from Aspinwall to Squaw Run, and beyond to Montrose, Powers Run, and Harmarville, without discovering additional localities for the species. Thus it seems that this locality is the only one on the northern side of the river, and we are able, as we shall see below, to explain its presence there.

This species is generally found at elevations from 900 to 1,200 feet; and it rarely descends to 800 feet or less. The lowest altitude at which it was found is 790 to 800 feet at Colliers, Brooke County, West Virginia, and at about the same (estimated) elevation it occurs in Fern-Hollow and Nine-Mile Run, Pittsburgh.

b. Origin of the distribution of C. monongalensis.

The distribution of this species outside of the state is very incompletely known, and consequently we cannot form any opinion as to its center of dispersal. Considering, however, that it is clearly a form cognate to *C. carolinus*, we may safely assume that it also came from the south, from West Virginia. *C. carolinus* and *C. monongalensis* seem to be two parallel species, closely connected genetically, the one belonging to the Old Tertiary base-level within the mountains, (elevation 1,200 to 2,000 feet), the other to the hills west of Chestnut Ridge (elevation 900 to 1,200 feet), formed by the Tertiary erosion of this base-level. The areas of both are separated by the escarpment of the Chestnut Ridge, and both have probably migrated on parallel lines.

C. monongalensis must have invaded Pennsylvania and the Panhandle of West Virginia from the south, being confined to the region between the Chestnut Ridge and the Ohio River. That in this case a large river forms a barrier to an aquatic creature is highly interesting, but is easily explained by the ecological habits of the species. Living underground near springs, and positively avoiding even the smaller streams, it is clear that a large river does not offer congenial conditions, and that it even may become dangerous to single individuals when they are accidentally swept into such a stream, they then being unable to get out and reach more favorable locations.

The restriction of this species to a comparatively small area in southwestern Pennsylvania is thus easily explained. The northward expansion was stopped by the first large river flowing from east to west in this region.

A few additional points need discussion. Coming from the south, this species migrated largely in the direction of the great tributary of the Ohio, the Monongahela, and this river did not offer a barrier. It is different with the Youghiogheny. The latter comes through the Chestnut Ridge, and should form a barrier to the east, preventing it from entering Westmoreland County and eastern Allegheny County, On the other hand we see that this species has in one instance crossed the Alleghany River. I do not think that this is due to direct and actual crossing of the rivers, but to a shifting of their courses, of which we have many evidences. The geological history of the rivers of this region is as follows. The highest elevations of the country between Chestnut Ridge and the Ohio River are very uniform, rarely going beyond 1,200 or 1,300 feet. This seems to represent an old base-level, belonging to Old Tertiary times, according to Campbell (1903, p. 292 ff.). This was again cut into by a drainage system belonging to the Old Monongahela or Spencer River, which, at the end of the Tertiary, was running again at base-level (White, 1896, p. 377), at an elevation of about 900 feet (in the region of Pittsburgh), having eroded its valley about 300 feet below the Old Tertiary base-level. This river was rather sluggish and frequently formed ox-bows. The most important old channels, having regard to the matters in hand, are in the first place those which are marked by a terrace about 225 feet above the present river (at Pittsburgh), both along the Youghiogheny and Monongahela, at McKeesport, Allegheny County, to the east of the present rivers, which, consequently, have been shifted to the west (Jillson, 1893, p. 12, pl. 1). East of Pittsburgh we have an old ox-bow of the Monongahela in the "Wilkinsburg Valley" at about the same level (Jillson, ibid., p. 8 ff.). Here also the river has been shifted to the west. These instances are sufficient to show that repeatedly and at various places opportunities were offered to *C. monongalensis* to passively cross the Youghiogheny and the Monongahela Rivers on account of the shifting of the latter, and the same seems to be the case with reference to the Allegheny River in the region of Squaw Run. According to Jillson (l. c., p. 10), there is a terrace 250 feet high belonging to the same general level as those mentioned above, one to two miles north of the Allegheny in the region of Claremont. At the same place there is another terrace north of the river, only 150 feet high, and consequently belonging to a later period, so that here the final shifting of the river to the south took place later than in the other cases.

These facts, if they at all influenced the distribution of *C. monongalensis*, and I believe they did, give us a hint as to the time of the immigration of this species. The shifting of the rivers must have taken place sometime during the Glacial Period, for we know that during this time a considerable amount of erosion was accomplished, the 900 feet level belonging to the beginning of the Glacial time (Lake Monongahela stage).[62]

This leads us to the conclusion that *C. monongalensis* must have been present in this region during the Glacial Period, at least during a part of it, and shortly before these channels were changed.[63] It is quite possible that this species had its preserve in Glacial time not far from the edge of the ice in southern Pennsylvania and northern West Virginia, and that it began to advance as soon as the ice of the Wisconsin stage began to recede. This would fully explain the fact that this species was able to cross first the Youghiogheny and Monongahela by the help of the westward shifting of these rivers, thus opening a way into eastern Allegheny and Westmoreland Counties, and that it later crossed the Alleghany River at Claremont, when its channel was changed to the present more southern position.

The question remains, why *C. monongalensis*, having crossed the Alleghany, did not advance further north. It is found at Claremont (near Squaw Run), in a comparatively restricted locality, which is not altogether favorable, being at a rather low elevation. It has not been able to reach more favorable locations at higher levels, the ascent being more or less difficult on account of the very precipitous hillsides, and moreover it may not prosper here because of the presence of the competing species, *C. diogenes*, which is quite abundant in this region. *C. monongalensis* is here, so to speak, cornered, and surrounded by unfavorable physical, ecological, and biocenotic conditions.

If this species existed in this region during Glacial times its Preglacial origin becomes rather probable. This is in keeping with the morphological characters, as compared with *C. diogenes*, for the latter, as we shall see below, is very likely also preglacial.

---

[62] The rivers were cut down even deeper than they are at present, but the valleys were filled up again, 100 feet or more (see Jillson, l. c.). According to Foshay (1890, p. 402), the chief erosion falls into the end of the Tertiary; but the presence of glacial material in the old river channels, 900 feet high (East Liberty, Pittsburgh), places the deepening of the valleys at a later period. Possibly it was connected with and subsequent to the draining off of Lake Monongahela (White, 1896, p. 375), which happened sometime during the Glacial Period. Hice (1903, p. 229) places this cutting down below the present channels between the Kansan and the Wisconsin stages.

[63] The same conclusion is reached when we consider that this species cannot have immigrated before the present Ohio was formed, that is to say, shortly before the Wisconsin stage (see last footnote). Otherwise the Ohio would not form its western boundary.

We have no evidence as to the Preglacial history of *C. monongalensis*. It may, however, be said, that it must have come from the original home of the subgenus *Bartonius* in the southern Appalachians. How far north it extended in Preglacial times we do not know, but the advancing ice cannot have driven it back very far. This is very probable because it is a form decidedly partial to cold water. With reference to its Glacial-Postglacial migration it belongs to the *northeastern biota* and the *second wave* of Adams; but its advance was apparently checked at an early date by the Ohio-Allegheny River.

It will be remembered that with reference to *C. carolinus* another view has been expressed (p. 453). In the case of that species we do not possess any facts which enable us to fix its time of immigration into Pennsylvania with the same probability as in the case of *C. monongalensis*. The present extension of the range of *C. carolinus* in the southern mountains classes it rather with the *southeastern biota*. On the other hand, we know nothing about the southern range of *C. monongalensis*, and thus it is at present impossible to properly compare these two species. Their close affinity, however, and the identity of the ecological conditions under which they are found (aside from the difference in altitude) render it rather probable that the parallelism observed between them in some respects may reveal itself also in others.

7. *Cambarus diogenes.*

a. *Summary of facts.* (See pp. 405–407.)

Aside from a narrow strip along the Delaware River, in Delaware, Philadelphia, and Bucks Counties in eastern Pennsylvania, this species covers a large area in southwestern Pennsylvania, namely all the region occupied by *C. monongalensis*, and, in addition, a belt of a certain width to the north of it (see Pl. XLIII). Here the eastern boundary is formed, as in the case of *C. monongalensis*, by the Chestnut Ridge, but it is continued beyond the Loyalhanna River, extending into Indiana County, and then it follows the divide between the Susquehanna and Allegheny drainages as far north as the southern extremity of Jefferson County. From this region the boundary runs in a westerly direction.

In Jefferson County I found this species at Punxsutawney, and I have seen chimneys rather abundantly to the east of this place, when riding on the Buffalo, Rochester, and Pittsburgh Railroad, about as far as Big Run, Jefferson County. But this species is not present in the neighborhood of Du Bois and Falls Creek in Clearfield County, although favorable localities are numerous there. In the valley of Red Bank Creek I have looked for it in vain near Brookville, Jefferson County. Further west the boundary becomes obscure, and is marked by the following localities: Kittanning in Armstrong County; Renfrew and Branchton in Butler County; and Mercer in Mercer County. At all events I found this species at the places named, but not north of them. Since no apparent physical feature marks the boundary in these parts, it remains doubtful whether this is the actual northern limit of distribution; but we can narrow down the zone in which it must be situated by naming a few more northern places where I searched for it in vain at the proper places: Goodville, Indiana County;[64] Templeton, Armstrong County (swampy places of the Alleghany river-bottoms); Oil City, Venango County; the region of the Pymatuning Swamp near Linesville and Summit, Crawford County. It seems, however, that toward the west the boundary has the tendency to run in a northwesterly direction, and in Ohio this species reaches the Lake Erie drainage in Lorain County (Oberlin).

Within the region above defined this species is generally found at a slightly lower altitude than *C. monongalensis.* It is, however, not preëminently characteristic of the river-bottoms, as I formerly believed (1905*a*, p. 400), but is chiefly distributed at an elevation of about 900 feet (more or less), that is to say, at about the level of the valley of the Old Monongahela River of Preglacial times. At the foot of the Chestnut Ridge it goes up to 1,200 feet and more, the highest point being Donohoe, Westmoreland County, 1,260 feet, but on the other hand it descends to the river-bottoms, between 600 and 700 feet, the lowest elevation observed being on the Ohio river-bottoms at New Martinsville, West Virginia, about 600 feet. Thus *C. diogenes* is quite abundant at about 900 feet, where *C. monongalensis* is decidedly rare; above this *C. diogenes* is rare, while *C. monongalensis* has its chief domain at this level; and below 900 feet *C. diogenes* is also abundant, while *C. monongalensis* is found only in exceptional cases.

While the boundaries of this species in Pennsylvania are tolerably well known, it is quite different with the rest of the range. It appears that the range is divided into two unequal, discontinuous parts, an eastern and a western. The eastern comprises, aside from the small section of Pennsylvania along the Delaware River, the whole or portions of New Jersey, Delaware, Maryland, the District of Columbia, Virginia, and North Carolina. Here it seems to be found exclusively in the Coastal

---

[64] This is in the same valley as at Punxsutawney, but *C. diogenes* is positively not found here, since a splendid place was found for it where it ought to have been discovered if at all present in the neighborhood.

Plain, not even entering the Piedmont Plateau. The western range begins in southwestern Pennsylvania and northern West Virginia, and we have seen that it here belongs chiefly to the late Tertiary base-level of the rivers. But in Pennsylvania it has entered the glaciated area (Lawrence and Mercer Counties), and thence has spread westward over the states of Ohio, southern Michigan, Indiana, Illinois, Wisconsin, southern Minnesota, and Iowa. Its main range is here in the glaciated region. But it also occupies localities south of the drift, in Indiana, Kentucky, Illinois, Missouri, Kansas, Arkansas, Mississippi, and Louisiana, extending westward to Colorado.

b. Origin of the distribution of C. diogenes.

The first point to be ascertained is whether there is actual discontinuity between the eastern and western range of this species. In western Pennsylvania I have positively located an eastern boundary for this species. It is formed by the divide between the Susquehanna and the Alleghany in the north, further south by the Chestnut Ridge. In the northern parts of West Virginia I am also positive that it is not found east of the Chestnut Ridge in Preston and Tucker Counties. We have the report of Faxon (1885*a*, p. 71) that this species is found at Deer Park, in western Maryland, but, as we have seen, this is erroneous (p. 406, footnote 27), and the species is absent in this whole region. I have searched for it in vain in Somerset and Fayette Counties (east of the Chestnut Ridge) in Pennsylvania, in Preston, Tucker, and Mineral Counties, West Virginia, and in Garrett and Alleghany Counties, Maryland. East of the Alleghany Front, in the Alleghany Mountain region, in the Great Alleghany Valley, and the Piedmont Plateau it is positively absent. It has never been recorded from anywhere within these physiographical divisions, and I myself made special search for it in Bedford, Blair, Fulton, and Franklin Counties, and in the eastern section of Pennsylvania, and further in the Potomac valley at Cumberland and Hancock, Maryland, and Cherry Run, West Virginia. At many of these places highly favorable localities were discovered, but no chimney-builders were found. This is the more convincing since I succeeded with ease in demonstrating the presence of this species on the alluvial flats of the Delaware River in Pennsylvania.

Although our knowledge of the distribution of *C. diogenes* in Virginia and North Carolina is far from being complete, all known localities are on the Coastal Plain, and thus it appears that there is actually a gap in the distribution formed physiographically by the Appalachian system and the Piedmont Plateau.

Our knowledge of the distribution in the west is also very defective, and more particularly we do not know anything about its southern boundary in West Virginia and Kentucky. Thus it is difficult or impossible to arrive at any conclusion as to its center of dispersal. But at this point certain morphological observations may possibly afford some help. We have seen (p. 407) that in western Pennsylvania the areola is often not entirely obliterated, a condition which is certainly more primitive than the normal one. Such specimens are quite frequent in southwestern Pennsylvania, while in the other parts of the range they are rather rare or entirely absent. This fact, according to Adams' (1902, p. 122, 125) eighth criterion for the determination of centers of dispersal, points clearly to southwestern Pennsylvania. Here the character of the areola is the least progressive, while in either direction from this center, to the east and to the west, it is more progressive. This conclusion is further substantiated by Adams' seventh criterion: "location of least dependence upon a restricted habitat." We do not know much about the "habitat" of *C. diogenes* in the west and south, but it is certain that in western Pennsylvania it is less restricted than in eastern Pennsylvania. Along the Delaware River I found it exclusively in the black muck of the alluvial flats, while in western Pennsylvania it has a much wider range ecologically, being found in clay bottoms, on hillsides, near springs, swamps, and even on sandy or gravelly soil.

Judging from these facts, and also from the general rule which holds good for the subgenus *Bartonius,* that its center is in the Appalachian region, we may safely assume that *C. diogenes* did not have its center on the Atlantic Coastal plain, nor in the western parts of its range in the Mississippi basin, but that it is somewhere on the Alleghanian Plateau; and since southwestern Pennsylvania and northern West Virginia are the only parts of this plateau occupied by this species, we have to place its center here.

Here, as we have seen, it dwells chiefly upon the late Tertiary base-level of the Old Monongahela drainage, and I believe this was its original habitat. We have no means to decide whether it was already present in this region in late Tertiary times; but the simple fact that it does occupy an area, the physiographical features of which have developed in Tertiary times, is in favor of this assumption. Further on we shall become acquainted with another reason for this view. In the Tertiary period its range very likely extended further north; but the Glacial Period must have restricted it, and its preserve was in the region indicated. In Postglacial times it spread northward again, at least in Pennsylvania. Unlike *C. monongalensis,* the rivers did not form a barrier, for this species largely descended into the valleys, going down to the river-bottoms and the very banks of the river,[65] and thus it should have been able to cross the latter. Consequently its range extends beyond that of *C. monongalensis.*

---

[65] It is found frequently on islands in the rivers (Neville and Twelve Mile Islands, near Pittsburgh). I have seen chimneys on the river banks near Verona, and obtained specimens on the banks of the Kiskiminetas at Kiskiminetas Junction.

It is doubtful what physical feature constitutes the northern boundary of this species. In Jefferson, Armstrong, and northern Butler Counties, where the boundary is apparently located, the late Tertiary base-level, to which this species belongs, loses its identity. Possibly it was not developed at all, and this region was not reduced to base level. So it might be possible that the roughness of the country constitutes a barrier here, and this is supported by the fact that the boundary is located further south in the Alleghany valley than to the east and west of it. On the plateau-like regions in Indiana and Butler Counties, favorable localities are abundant, while the narrow Alleghany valley, with the deeply cut valleys tributary to it, do not offer congenial conditions.

It is different further west. In Lawrence and Mercer Counties this species has invaded the glaciated area, and is found to the north of the terminal moraine (see Lewis, 1884, p. 183 and 193, Pl. 11 and 12), and here prefers the swampy depressions formed by kettleholes. But a northern barrier at this point is not evident, although a tendency to a northward extension seems to be indicated.

Having thus invaded the area of the drift, it is not astonishing that this species spread over large tracts of the latter in Ohio, Indiana, and Illinois. Its presence to the south of the drift in the Mississippi Valley would then be a continuation of this westward migration, which finally varied toward the southwest and the south. I have represented it as such (Ortmann, 1905*b*, p. 123, Pl. 3) in a previous paper. Nevertheless this question needs further investigation.

There remains the eastern area of this species on the Atlantic Coastal Plain. In the paper just referred to I have expressed the opinion (*l. c.*, p. 123) that it "descended from the mountains" toward the east, but this apparently needs correction. Of course the direct way from its supposed center to the Atlantic plain is from southwestern Pennsylvania and northern West Virginia across the Appalachian system and the Piedmont Plateau to Maryland and Virginia. But the total absence of this species from this region is against this assumption. There is no possible reason why it should have disappeared from the Potomac valley, if it had once been present there, favorable localities being abundant.

Comparing, however, the present eastern range of *C. diogenes* with that of *C. limosus,* we are struck at once by the general similarity. Both species belong to the Coastal Plain from New Jersey southward, *C. diogenes* going a little further south, and not quite so far north, while *C. limosus* has entered the Piedmont Plateau, and *C. diogenes* has not. This similarity induces us to assume a similar origin of distribution, and in that case *C. diogenes* would also have come from the north, being driven back by the advancing ice.

This necessitates the further supposition that *C. diogenes* is a Preglacial species (another reason for this has been mentioned above), which extended before the beginning of the Glacial Period further north, probably from western Pennsylvania into New York or even beyond. This is not improbable, since the Alleghany Plateau stretched considerably to the north in Preglacial times (see Powell, 1896, p. 80), and although the Preglacial features are largely obscured in this region, it might have been possible for this species to cross over into the coastal plain from western New York to southern New England or northern New Jersey, skirting the northern extremity of the Appalachian system. The coming of the ice must then have resulted in the obliteration of the northern connection of the range, thus dividing the originally continuous area into a western and an eastern subdivision.

According to Adams' classification (1905, p. 58), *C. diogenes* belongs to the *north-eastern biota*, but its dispersal in Postglacial times does not entirely agree with that of the *second wave*. Indeed there is a slight indication of a northward advance in Pennsylvania, Michigan, Wisconsin, and Minnesota, but the main direction was *westward* from the Alleghany Plateau, and even *southward*. This is undoubtedly due to the ecological peculiarities of this species (chimney-builder), it having found no competition in the directions named. In the eastern section of its range a northward advance is hardly noticeable. Here the species is more restricted ecologically (apparently a higher specialization), favoring only the black mud of alluvial deposits, and this very likely prevented its northern expansion. However, its exact distribution in New Jersey is unknown.

8. *Summary of the Studies on Geographical Distribution.*

We have been able in the preceding studies to advance a theory for the dispersal of each of the Pennsylvanian species of crawfishes. It cannot be denied that in certain points our ideas do not seem to be well supported, but this is chiefly the case in instances where our knowledge of the extralimital distribution is defective. It is to be hoped that similar investigations outside of our state may furnish additional evidence to substantiate our conclusions, or if necessary, to modify them. This much, however, is evident, that the facts of the distribution of our species are due to two causes: (1) partly to the existing physiographical features of the country; (2) partly to past conditions, which have now disappeared. On the accompanying map (Pl. XLIII), we notice the following particulars. In the eastern part of Pennsylvania, along the Delaware River from Trenton, N. J., to Marcus Hook, Delaware

County, a small part of the *Atlantic Coastal Plain* enters the state. The Delaware River runs along the escarpment of the Piedmont Plateau ("fall line," See McGee, 1888, p. 122), but at several places a narrow space is left, chiefly opposite Trenton, in Bucks County, and below Philadelphia, where alluvial flats are found. These we may include in the coastal plain, and they are characterized by the presence of *C. diogenes* (together with *C. limosus*).

The next physiographical divisions of Pennsylvania are the *Piedmont Plateau* and the *Great Alleghany Valley*, reaching from the eastern escarpment of the former to the Blue Mountain. These divisions form a unit in Pennsylvania. The dividing line between them, South Mountain, being rather insignificant and obliterated, chiefly toward the northeast.[66] This fact is also expressed to a certain degree in the distribution of the crawfishes. Aside from the generally distributed *C. bartoni*, we have here *C. limosus*, which has invaded this region, coming from the lower Delaware, Susquehanna, and Potomac. It seems to have spread all over the Piedmont Plateau, and also into parts of the Great Alleghany Valley, for instance, into the Cumberland Valley (between South Mountain and the Blue Mountain, called here the North Mountain, in Franklin and Cumberland Counties). It has also been found in the Schuylkill and its tributaries in Berks County, but not as yet in the Lebanon and Lehigh Valleys (northeastern continuations of the Great Alleghany Valley). Whether the conditions presented here are original or not seems doubtful. On the one hand it may be that the canals have served to distribute this species; on the other hand, pollution of streams may have restricted it. Be this as it may, the fact remains that the physiographical divisions distinguished as the Piedmont Plateau and the Great Alleghany Valley possess a species of crawfish which is not found elsewhere, except in the Coastal Plain and the Susquehanna Valley.

Then follows the *Alleghany Mountain* region, between the Blue Mountain and the Alleghany Front (see Willis, l. c.). In the southern and central parts of the state this section is well marked. In the northern part its western boundary is obliterated, the Alleghany Front losing its identity. But all the areas which undoubtedly belong to the mountain region are uniformly characterized by the presence of only the one species, *Cambarus bartoni*, with the exception that *C. limosus* is found in the middle Susquehanna valley from Harrisburg upward to Columbia and Center Counties, and in the Juniata valley up to Bedford County; and further, *C. obscurus* exists in Wills Creek, Bedford County. Both these exceptional cases, however, do not represent, in my opinion, original conditions. This is most evident in the case of *C. obscurus* in Wills Creek, where no other explanation is possible except that of artificial introduction. With reference to the occurrence of *C. limosus* in the middle Susquehanna and the Juniata, within the Alleghany Mountains, I think in this case also a recent immigration took place, favored by artificial means (canals). This is, however, somewhat doubtful, since it is impossible at present to ascertain the normal and original conditions prevailing in eastern Pennsylvania before modern improvements were introduced.[66a]

---

[66] See Willis, 1896, p. 172, and map p. 170–171. South Mountain is the continuation of the Blue Ridge of Virginia, while the Blue Mountain of Pennsylvania is not identical with the Blue Ridge, but is to the west (northwest) of it.

The region containing only *C. bartoni* goes beyond the boundary of the physiographical division of the Alleghany Mountains. In the northwest the Susquehanna has captured a large part of the drainage of the Alleghany Plateau, and the whole basin of the West Branch of the Susquehanna is included in the section containing only *C. bartoni.* But again a physiographic boundary is formed by the divide between the Susquehanna and Alleghany river-systems.

All the rest of the state belongs to the *Alleghany Plateau.* Here much more varied conditions prevail with regard to the distribution of crawfishes, and this is chiefly due to the fact that this region was open to Preglacial and Postglacial immigration from the south, southwest, west, and northwest. Aside from *C. bartoni,* which is found everywhere, the following five species immigrated into this region: *C. propinquus, C. obscurus, C. carolinus, C. monongalensis,* and *C. diogenes.* Since each of these species had a different center of radiation, a different geological history, different ecological habits, and since, consequently, different barriers existed to the dispersal, no two species possess the same range.

C. propinquus came from the west and northwest in Postglacial times. It belongs to the Erie basin, and is restricted by the divides of the latter. Thus it is confined in Pennsylvania to the Lake Erie drainage in Erie and Crawford Counties.

C. obscurus belongs to the Preglacial Spencer River or Old Monongahela, and to Lake Monongahela of early Glacial age. The Postglacial dispersal includes first of all the Ohio-Monongahela-Alleghany drainage, and thus generally the divides of this basin constitute its boundaries, with a few exceptions. In the region of the upper Youghiogheny and the Conemaugh the roughness of the streams has prevented it from reaching the plateau to the east of the Chestnut Ridge. In Crawford and Erie Counties it has crossed over into the Erie drainage (due to stream-piracy or to artificial means), and in Potter County it has found a way into the Genessee system (due to stream-piracy).

C. carolinus came from the south, along the high level plains of early Tertiary

[66a] The green color on the map, Pl. XLIII, should be continued up the Juniata to Bedford County.

age, being partial to extensive clay bottoms. Such conditions are found well developed only between that part of the Alleghany Plateau which is enclosed between the Alleghany Front and the Chestnut Ridge. Possibly also elevation has played a part. Thus it is found only in Somerset and parts of Fayette and Westmoreland counties. The northern boundary is formed by rather insignificant and possibly temporary barriers.

C. monongalensis is a form parallel to *C. carolinus.* It also came from the south, and invaded southwestern Pennsylvania, keeping to locations of less altitude than *C. carolinus.* Thus its eastern boundary is formed by the Chestnut Ridge. Its northward advance was checked by the first large river flowing east and west, namely, the Loyalhanna-Kiskiminetas-Alleghany-Ohio.

C. diogenes seems to be similar, at least in western Pennsylvania, to *C. monongalensis,* but it was able to cross the rivers northward. The northern boundary is obscure, and may be not entirely due to topographical conditions. Attention may be here called to the fact that the isotherms have a curve somewhat similar to that formed by the northern and eastern boundary of this species.

Thus western Pennsylvania is divided into several sections characterized by their crawfish-fauna, namely:

1. Area of *C. carolinus* (containing *C. bartoni* and *carolinus*): Somerset and southeastern Fayette Counties.

2. *Area of C. diogenes and C. monongalensis* (containing *C. obscurus, bartoni, monongalensis,* and *diogenes*): Greene, Washington, northwestern Fayette, western Westmoreland, southern Allegheny, and southern Beaver Counties.

3. *Area of C. diogenes without monongalensis* (containing *C. obscurus, bartoni, diogenes*): northern Beaver, northern Allegheny, northeastern Westmoreland, western Indiana, southern Jefferson, southern Armstrong, southern Butler, Lawrence, and southern Mercer Counties.

4. *Area of C. obscurus* (containing *C. obscurus* and *bartoni*): northern Jefferson, northern Armstrong, northern Butler, northern Mercer, the largest part of Crawford, Venango, Clarion, and Forest, western Elk, northwestern Potter, McKean, Warren, and southeastern Erie Counties.

5. *Area of C. propinquus* (containing *C. propinquus, obscurus, bartoni*): northern and western Erie and a small part of Crawford Counties.

These are the chief divisions, but there are a few minor differentiations. The greatest variety prevails in Westmoreland County. Its western part (west of the Chestnut Ridge) belongs to two of the above areas (2) and (3), divided by the Loyalhanna River. But besides the valley between the Chestnut and the Laurel Hill Ridges presents three different conditions, namely:

(*a*) Conemaugh drainage, with only one species: *C. bartoni.*

(*b*) Ligonier Valley, with two species: *C. bartoni* and *obscurus.*

(*c*) Headwaters of Indian Creek, with three species: *C. obscurus, bartoni,* and *carolinus.* This latter section also comprises the northeastern corner of Fayette County.

The greatest number of species found in any one county is five, namely, *C. obscurus, bartoni, carolinus, monongalensis,* and *diogenes.* This is the case in Westmoreland and Fayette Counties. They may be found in close vicinity only along the escarpment of the Chestnut Ridge. For the rest *four* is the largest number of species found closely associated, namely the four belonging to the second area, comprising the range of *C. monongalensis.*

In conclusion, attention should be called to the fact that the terminal moraine in no case constitutes a barrier for any of the Pennsylvanian crawfishes. (Compare Lewis' map, 1884, with our maps, Pl. XLII and XLIII.) Of course, for the river-species the moraine would not be of any consequence, and of the burrowing species, two, *C. carolinus* and *C. monongalensis,* do not reach it at all, while *C. diogenes* has crossed it in the west. But instead of being a barrier the glaciated area rather seems to offer more congenial conditions on account of the frequency of swampy places (kettleholes).

The question remains, whether our survey of the state is to be regarded as complete and exhaustive, or whether there might be other species within its limits. This is suggested by Faxon (1885*a*, p. 165) as to *Cambarus blandingi* (Harlan). This species is found in New Jersey at Trenton, on the Delaware meadows just opposite the eastern extremity of Bucks County, Pennsylvania, associated with *C. limosus* (Faxon, l. c., p. 22 and 88). I have made a careful search for it in this part of the state, and visited this corner twice (Sept. 15, 1904, and at the same date, 1905). Having collected this species previously in New Jersey, I was acquainted with its ecological habits and knew where to look for it. I indeed found localities that appeared favorable, but I failed to see any traces of the species. I think it is quite safe to assert that this species is not found in this state.

The case of Lake Erie is a little different. We have records showing that in Ohio the western extremity of the lake is inhabited by *Cambarus rusticus* Girard and *C. immunis* Hagen. The former has been reported from Kelley's Island (Faxon) and from Sandusky Bay (Osburn and Williamson), and from several tributaries of the lake. The latter is mentioned from Lake Erie, off Lorain County (Osburn and Williamson), and from tributaries of the lake as far east as Lorain County. *C. rusticus* is not found anywhere further east, and it seems doubtful whether it finds congenial conditions *in* the lake. The specimens taken may have been accidentally swept into the lake. Thus I do not believe that it will be discovered in the part of the lake bordering upon Pennsylvania.

C. immunis, however, besides being found in northern Ohio, reappears in New York. Faxon (1898, p. 654) has recorded it from a tributary of Oneida Lake, and recently I have seen specimens, belonging to the New York State Museum, collected by Mr. F. C. Paulmier in Rensselaer Lake, Rensselaer County. Thus its presence in New York, upon which I cast some doubt (1905*b*, p. 134), is to be regarded as firmly established. However, the connection of these eastern localities with the western range has not been discovered. If a connection is present at all, it is to be looked for in the Erie-St. Lawrence basin, and thus would possibly include the lake shores of Pennsylvania. Yet this connection may not exist, and *C. immunis* in New York may be a recent, artificial introduction, which is not altogether impossible, since we know that the crawfishes used for food in the New York market come in part from the lake regions (Milwaukee, see Ortmann, 1900, p. 1260), and thus this species may have been introduced. But this question is by no means settled, and we should try to obtain further facts.

Finally we may observe that the conditions now existing in the case of the Pennsylvanian crawfishes may not be original, but may have been altered by human agency. The possible influence of canals upon the dispersion of two species, *C. limosus* in the east, and *C. obscurus* in Crawford and Erie Counties, has been discussed in the foregoing pages, and the transplantation of *C. obscurus* into Wills Creek has been stated to have apparently occurred, accidently or intentionally, through human agency. No other cases of dispersion beyond the natural boundaries by artificial means are probable. But on the other hand certain species may have become extinct, at least in parts of their original range, through human agency. Of this we have many instances, but in our state none has gone so far as to entirely obscure the original conditions. We have pointed out above that the absence of *C. limosus* in the Delaware and Schuylkill Rivers in the region of the Great Alleghany Valley may be due to the pollution of the streams issuing from the anthracite region. That these rivers, as well as the Susquehanna are considerably polluted partly by city sewage, partly by mine-water, is sure (see Leighton, 1903, p. 112, and 1904, p. 48), but whether the absence of *C. limosus* in this region is due to this fact, or not, cannot be settled.

It is different in the western part of the state. Here *C. obscurus* originally occupied all of the Monongahela and Alleghany drainages west of the Chestnut Ridge, but there are many streams in which it is now lacking, and in which we must assume its former presence. This is apparently due to the large amount of pollution in these streams, chiefly by water from mines. The pollution of the Alleghany River near Pittsburgh, although bad enough from a sanitary standpoint, and due in the first instance to sewage (Leighton, 1903, p. 122) does not affect the crawfishes, for they are very abundant here, and the Ohio below Pittsburgh is rich in crawfishes. But there are many smaller streams contaminated by the waste of coal-mines.[67] Such streams are recognized at a glance by the precipitate of reddish and yellowish sulphate of iron upon their bottoms, and are invariably without life. This is most evident in the Monongahela drainage of southwestern Pennsylvania (Washington, Fayette, and southern Allegheny Counties), and also in many smaller streams in Butler, Westmoreland, Indiana, and Jefferson Counties, where coal-mines are abundant. The worst conditions prevail in certain tributaries of the Monongahela, in the Monongahela itself, in the Loyalhanna below Latrobe and the Kiskiminetas, and in Red Bank and Sandy Lick Creeks. The Clarion River is also without crawfishes in Jefferson and Elk Counties, but this is due chiefly to pollution by sewage from wood-pulp mills and tanneries (see above, p. 443). In all these cases it is evident that *C. obscurus* once existed here, since remnants of it are left at many places in some of the clearer and not polluted side streams. Since this pollution of the streams by coal-mines is bound to increase, *C. obscurus* certainly will disappear from other streams. As we have seen above it was on the point of dying out in Sandy Lick Creek at Du Bois in 1905 (p. 443, footnote 58). Another case has been observed in Fern-Hollow Run, Pittsburgh. In the fall of 1903 I found a small number of specimens of this species left over in some pools once connected with the run; a sewer had recently been built here, discharging its polluted water into the run. In subsequent years this species was not again seen, and has entirely disappeared, as also from Nine-Mile Run, which receives sewage from Wilkinsburg and Edgewood.

It should be added that *C. bartoni* also is frequently influenced by the contamination of streams, but seems rather more resistant than *C. obscurus*. In two cases this was evident, namely, in Mahoning Creek at Punxsutawney, and in Slippery Rock Creek at Branchton. In both cases the streams were only slightly polluted by mine-water, and contained a certain number of specimens of *C. bartoni*, while *C. obscurus* was absent. The latter existed at Punxsutawney in a pond connected with the stream, and at Branchton in a smaller clear tributary, and consequently must have once been present in the two creeks.

A stream or river polluted in a certain part becomes relatively clear and pure again further down. This is generally seen in the Ohio below Pittsburgh. Although the Ohio collects all the badly polluted streams of western Pennsylvania, it is itself not unfavorable to crawfish life. The best instance for this is the Cheat River. At Cheat Haven, Fayette County, this river is rather clear and teems with life, crawfishes and *Unionidæ* being abundant. I was therefore astonished at the condition of this river at Parsons, Tucker County, West Virginia. The water there has a foul smell, and is utterly unfit for life, which is due to a wood-pulp mill just above Parsons on Shavers Fork. Between Parsons and Cheat Haven (about fifty miles) the water has improved so far that life is not only possible, but is abundant, only the blackish color of the water remaining as the last result of the contamination.

---

[67] As to the chemical processes going on in the so-called "sulphur water," see Leighton, 1904, p. 24.

V. LIFE HISTORY.

Only a few scattered notes have been published on the life-history of any of the American species of *Cambarus*, and some of them are rather doubtful. The most complete account is that given by Andrews (1904) on the breeding habits of *C. limosus*, but even this comprises only a small part of the life-history, and moreover, as may be seen below, is in part rendered unreliable by the fact that the observations were not made in the field, but in the laboratory.

My own observations have been almost exclusively made in the field, and were only occasionally supplemented, or rather confirmed, in the laboratory. Since it was my object from the beginning to watch the behavior of the crawfishes under natural conditions, laboratory-work could not be depended upon, unless controlled by field-work, and thus the former was neglected altogether.

With the exception of January and February,[68] my work in Pennsylvania extends over the whole year, thus including all seasons. The results are rather satisfactory, and I am able to give a complete account of the seasonal life of no less than four species, and by comparison with these the life-history of the other species of this state may be inferred. Of course I have not been able to solve all questions. For instance the question of the frequency of moulting in one and the same individual remains open, since it can only be settled by observing the same individual continuously; but this is impossible in the field. Nevertheless I have found means to elucidate this question in other ways, although not with absolute accuracy.

The most numerous and most complete records I possess refer to the common river-species of western Pennsylvania, *C. obscurus*, and of this I shall first give an account.

---

[68] From New Jersey I possess observations made even in January and February and referring to *C. blandingi*, *C. limosus*, and *C. bartoni*.

1. *Cambarus obscurus.*

Nothing whatever was previously known in regard to the life-history of this species. I have observed it during the larger part of two seasons, the dates of actual observation covering the time from March 28 to November 19 (in 1904 and 1905).

Beginning in spring (March) it is ascertained that the species is at this time quite active, being found in the usual localities (under stones in rivers and streams), and the specimens are of various sizes and conditions, but all agree in having a rather dirty (mud-incrusted) shell, a sure sign that the shell is old and that no recent moulting has taken place. There are occasional specimens with a very clean shell, in which moulting has occurred quite recently. This teaches us that during the winter months as a rule moulting does not take place, but that it begins quite early in spring, although only in the case of a few individuals. Males of the first form are abundant at this time, while males of the second form are scarce, and it is chiefly these newly moulted males which are of the second form. It seems, however, that in exceptional cases rather young males (30 to 40 mm. long) may have gone through the winter in the second form. The size of the males of the first form varies greatly; the smallest found by the writer in spring (May 2, 1905) measure 40 mm. in length, but specimens between 40 and 50 mm. long are very abundant. All the males between 30 and 40 mm. long are of the second form, but they are not abundant, as has been stated. The smallest male found in spring was 31 mm. long. The condition of the females in early spring corresponds to that of the males, and in this sex the minimum size is 27 mm. in length.

Very soon an important event takes place in the life of the females. Eggs are laid. No signs of this were seen on March 28, 1905, and March 31, 1905, although a large number of individuals were collected at these dates. But on April 6, 1905, (in Thorn's Creek, Renfrew, Butler County), numerous specimens with eggs were taken, some in the very act of spawning. I was able to observe in this species the peculiar attitude assumed by the female, and the "apron," described by Andrews for *C. limosus* (1904, p. 180, fig. 5; p. 182, fig. 6). The same was seen repeatedly on subsequent dates in April, so that April is to be considered as the spawning season. The number of eggs is rather large, one hundred to two hundred and even more, but young specimens sometimes have considerably less.

From the beginning of April onward females with eggs are found very regularly until the end of May. My dates are the following: April 6, 1905; April 10, 1905; April 19, 1905; April 24, 1905 and 1906; May 1, 1905; May 2, 1905; May 3, 1899 (Williamson and Shafer); May 4, 1905; May 8, 1905; May 17, 1906; May 22, 1905; May 25, 1905. With one exception (April 15, 1905) I found females with eggs every time I collected this species during this period. This rather precisely fixes the time when the females are "in berry." They carry eggs during the months of April and May, but at no other time of the year, and during this season all females, with few exceptions, no matter whether they are large or small, have eggs. The smallest observed with eggs was 40 mm. long. Of course in the beginning of the spawning season larger females may also be without eggs, but later on females larger than 40 mm. long are only very rarely found without them. The latter generally are newly moulted (having soft or clean shells), showing clearly that at the beginning of the spawning season they were very likely below the minimum size for spawning. Of the few females under 40 mm. long none had eggs.

During the spawning season (April and May) a general tendency toward *moulting* is observed in all specimens which are not females "in berry." Among the sterile females, as well as among the males, the old, dirty shells disappear; newly moulted shells become more and more frequent, and soft shells are frequently observed. This moulting process in most individuals takes place in the first half of May, but, as we have seen, some individuals begin as early as March, and in others the process is delayed till the beginning of June. But by this time all specimens have moulted under normal conditions, with the exception of the fertile females, which moult after the young are hatched in June.

A remarkable fact in the case of the males is that this spring moult invariably changes them to the second form.[69] In consequence males of the first form become scarcer and scarcer, till finally at the beginning of June all have disappeared and only males of the second form are left. Another remarkable fact is that after the end of the moulting season in spring no very large males are found. While large males of the first form of over 70 and 80 mm. in length are quite abundant in March, April, and the first half of May, they become very rare after that time, and the males of the second form, which are then abundant, only in rare instances exceed the size of 70 mm. in length, (only two cases on record). During the summer the males are generally less than 70 mm. in length. Large males reappear after the summer and fall moults begin, and then they are again of the first form.

The question arises what becomes of the large males (over 70 mm. in length), which are rather frequent in spring. According to the records, we cannot assume that they moult into the second form, for we should then find large males of the second form in summer. Thus it is suggested that these large males die and disappear. Of this I have found positive evidence in two cases. On June 6, 1904, I collected in the Shenango River at Linesville, Crawford County, a large male of the first form, 81 mm. long, which was lying concealed under a rock in the usual position. It was absolutely perfect, without blemish, and with an old, very dirty shell, thus clearly showing that it had gone through the previous winter. This specimen was barely alive and to all appearances in a dying condition. A similar instance was noticed on April 24, 1905, in Wheeling Creek, Elm Grove, West Virginia. Here a large male of the first form (84 mm. long) was found showing no signs of injury, in fact in very beautiful condition, but barely able to move. It was kept in water, but was dead the next day, while other specimens collected together with it were none the worse for their journey to Pittsburgh. Thus it seems that the conclusion is justified that the largest males of the first form, after having in the autumn attained a certain maximum size, which may be different according to conditions, but may be said in general to be about 80 mm. in length, go through the winter, but do not moult again, and die a natural death in spring.[70]

---

[69] This change was first observed by Faxon (1884*a*, p. 42) in *Cambarus rusticus* Girard.

The latest dates at which I found males of the first form in spring are as follows: June 6, 1904, Linesville (the case just mentioned), May 30, 1904, at Waynesburg, Greene County; May 25, 1905, Alleghany River, Mosgrove, Armstrong County. After the beginning of June, all through the month, and through a large part of July, no males of the first form have been found, and through the remainder of July they are scarce. (See below.)

The eggs carried by the females hatch at the end of May and the beginning of June. I found young under the abdomen of the mother on May 30, 1904, on June 5, 1906, and on June 6, 1904. The period during which the young stay with the mother seems to be short. On May 25, 1905, I found eggs, not yet hatched. From June 15, 1905, onward all through the remainder of the year I never observed a female with eggs or young. Between these two dates I have only four records, May 30, 1904, June 2, 1905, June 5, 1906 and June 6, 1904, in three of which the presence of young ones with the mother was shown. Thus the period when young are found under the abdomen of the mother is very likely the end of May and first half of June (about three weeks), and the young crawfishes probably do not remain with the mother much longer than a week.

Throughout June and part of July no males of the first form are present; all males are of the second form, but they are not very large, reaching a maximum size of only between 60 and 70 mm. The females have got rid of their progeny, and begin to moult. The old females may die like the old males, but I have no evidence on this point, except as drawn from analogy to the males, and the fact that very large females are rare in the latter part of June and in July, and do not become more abundant till the beginning of August. In addition we now have a new generation of young crawfishes, hatched at the end of May and beginning of June. After these have left the mother it is difficult to get them. They are too small, and are often overlooked, and if captured in the net, are able to escape through the meshes. But I have seen them at this time, although the first recorded captures are as late as July 10, 1900 (by Dr. D. A. Atkinson), size 26 mm., and July 24, 1905 (by myself), size 21 to 23 mm. This young generation is easily distinguished from the rest by its size, being considerably less than 30 mm. in length. The minimum length of crawfishes in spring is 31 mm. in the case of males and 27 mm. in that of females.

---

[70] A great mortality of males in spring (after copulation in captivity) has been observed by Andrews (1904, p. 175) in *C. limosus*.

In the middle of July further changes occur. A new period of moulting begins for the medium-sized and older individuals, which is chiefly noticeable among the males, since they now again assume the first form. The earliest date for the new males of the first form is July 11, 1905 (Tionesta and Spartansburg). Altogether four individuals were taken, all of which had soft shells, showing the fact that they had recently moulted. Further dates are July 24, 1905 (Deer Lick), July 25, 1906 (Russelton), July 26, 1904 (Derry), July 27, 1906 (Shousetown), and then in August and the following months they regularly occurred. At first these males of the first form are scarce, but they become gradually more frequent, till finally at the end of September and in October almost all males have assumed the first form. This also holds good for the new generation born at the end of May and the beginning of June. These young ones are about 20 to 23 mm. long in July; in August I have specimens from 24 to 39 mm. in length; in September from 26 to about 50 mm. in length. About this time this generation becomes obscured; for it seems that the rate of growth of the young crawfishes is very different in different individuals, some gaining during June, August, and September, only about 15 mm. in length, others more than twice that length. They are about 10 or 11 mm. long when they hatch. The same fact was observed by Andrews (1904, p. 202) in *C. limosus*, with even greater differences in size (the length of the young of the same generation in October being between 22 and 60 mm.).

It is ascertained from the above observations that young specimens, born in early summer, already at the end of the first summer (September and October) reach a size sufficient to prepare them for propagation, and the males of this generation as a rule show this by changing into the first form. The smallest male of the first form, collected by myself in fall (October 6, 1905), is a specimen from Kittanning, 38 mm. long, but specimens from 40 to 50 mm. long, and undoubtedly belonging to this generation, are quite abundant at this time. Thus we see that by October the same conditions are established which were found in early spring. Males of the first form prevail, and those of the second form are scarce, and generally of a small size, between 30 and 40 mm. long. Specimens of less than 30 mm. in length are very rare and represented by individuals of the last generation, which have not been able for some reason to keep pace in growth with their brothers and sisters. The males are sexually mature, and apparently the females likewise, as we shall presently see.

Copulation actually takes place now. I have quite often observed it in the field; and made record of the following dates: September 5, 1906; September 28, 1905; October 6, 1904; November 19, 1904. In addition couples were found apparently preparing for copulation, but not in the act, on September 7, 1905, and September 30, 1905. Among the material collected by Mr. W. R. McConnell was a couple taken *in copula* on September 5, 1905. In captivity I observed copulation on September 8, 1905, and November 22 and 23, 1904, and I have found that it is very easy to induce couples to copulate about this time (September, October, November), provided that one male and one female are put in the same jar. In no other part of the year, and, what is more important, not even in spring (March, April, May) does copulation take place, either in nature, or in the laboratory. All my attempts to induce specimens to copulate in spring have been in vain, and, of course, in June, July, and part of August, copulation is impossible, the males not being in condition. Copulation may occur in August, males of the first form being present, but possibly the females are not in proper condition before September on account of the delay of the spring moult. The smallest female seen in copulation was 43 mm. long; and she undoubtedly belonged to the generation born in spring, thus establishing the fact that the females like the males are generally sexually mature at the end of the first summer, and that they are able to produce eggs the next spring. (*See above.* The smallest female with eggs was 40 mm. long.)

The above observations and conclusions are founded upon the comparison of large numbers of individuals, but no single specimen has been followed through all the different stages of seasonable development. But to a certain extent it is possible to ascertain the changes through which one and the same individual has to go, and to lay down its life history.

The young *Cambarus obscurus* is hatched at the end of May or the beginning of June, from eggs laid in April. The young stay with the mother under the abdomen of the latter, for a short time (about a week); then they shift for themselves and develop during the summer rather quickly, moulting repeatedly.[71] In September or October they have attained a length of from 40 to 50 mm., and the males have assumed the first form. The females also are sexually mature, and *copulation* takes place from September to November.[72] During the winter no changes occur, and in early spring they are in about the same condition as in the previous fall. In April the females *spawn,* and it is remarkable that spawning takes place normally from four to six months after copulation. The males generally go through the *spring moult* in May, the females a little later in June. This brings up the size of this generation to from 50 to 60 mm. Then the *fall moult* begins, lasting from August to October, in which the specimens attain a size of over 60 mm. After the first summer only two moults, the one in spring and the other in fall, seem to take place.

---

[71] Compare Andrew's observations on *C. limosus* (1904, p. 190, ff.): he distinguishes seven larval stages (each beginning with a moult), from the hatching, end of May, to the middle of July, when a length of 29 mm. was reached.

At about this time, (October of the second year), the specimens are seventeen months old. They go through a *second copulating season,* and through the following winter, and again through the spring and summer with the same changes, attaining by the two moults their maximum size of over 70 mm. in length. A *third copulating season* follows, their age being now two years and five months. After this they live until the next spring, when the old males die in April and May, and the old females probably in June. This shows the life of the individual to be about three years.[73]

This seems to be the usual life-cycle of this species. But there are exceptions, which are primarily due to the fact that in the first summer the growth of single individuals may be quicker or slower. Whether slow growth, inducing late develment, influences the total length of life cannot be ascertained, but it must lead to the result that some specimens are not sexually mature at the end of the first summer, and that thus the first copulation is postponed a whole year; for copulation seems to depend directly on the season, and takes place exclusively in fall, but never in spring. Furthermore it may be that in single cases life is prolonged an additional year, as for instance in exceptionally large individuals (about 90 mm. long). But we may safely assume that three years, or at the outside in exceptional cases four years, is the duration of the life of this crawfish, and that an individual that lives up to this age without having met with an accident has fulfilled its destiny and dies a natural death.

A few additional remarks should be made with reference to egg-laying, moulting, and copulation. The act of laying eggs is hard to observe, and I cannot improve upon Andrews' observations on *C. limosus* quoted above. The process of moulting, is also rarely observed. The old skin splits on the back, between the carapace and the abdomen, and the crawfish pulls itself out gradually, leaving the empty shell intact. I have not made any observations on the increase of size at the moulting time, in the case of this species. (But see below under *C. diogenes*, *monongalensis*, and *C. bartoni.*) None of my specimens kept in captivity went through this process, and those found in the field immediately after or during the act were too flabby to be measured. Empty shells have been found now and then, but the individuals belonging to these had then lost their identity. Possibly, as has been observed in *C. monongalensis*, the old shells are eaten up.

---

[72] Possibly beginning at the end of August and extending to January.

[73] Andrews (1904, p. 204) was able to trace *C. limosus* only to the third summer, when the sole survivor of his material reached the size of 90 mm.

The copulation resembles throughout that of *C. limosus*, as described by Andrews (1895, p. 867, and 1904, p. 166, Fig. 1, p. 168), and only a few remarks seem necessary. The male with its claws takes hold of the claws of the female at the base of the hand or the base of the fingers, and in shifting its position it often seizes several of the other pereiopods of the female. The other legs of the male are lying on the sides of the carapace of the female. All the legs of the female are lying close together on each side, directed forward. The male uses one of the fifth pereiopods, sometimes the right, sometimes the left, to elevate the copulating organs, and this leg is laid across the sternum, sticking out on the other side behind the fourth pereiopod. The use of the hooks is the same as in *C. limosus.*

After copulation the annulus of the female contains a "spermal plug," as described in *C. limosus.* Copulation takes place repeatedly between the same couple, and one male may copulate in succession with several females, and one female with several males. This has also been observed by Andrews (1895, p. 867) in *C. limosus*, who says copulation "may be repeated by either animal with some other."

2. *Cambarus propinquus and Cambarus propinquus sanborni.*

My observations on these two forms are fragmentary, but the dates at hand make it certain that the seasonal history is identical with that of *C. obscurus.*

For *C. propinquus* I have only three observations dated in the summer ; the most important being June 7, 1904 (Conneautville Station), when I collected a considerable number of this species. As in the case of *C. obscurus* no males of the first form were found, and all males of the second form as well as females were of medium size, between 47 and 60 mm. long. Specimens collected at the end of August, 1900, by Dr. D. A. Atkinson at Presque Isle were in the same condition (no males of first form), but there was with them a young female 27 mm. long, belonging apparently to the generation born in June.

The rest of my material was collected on October 4 and 5, 1904, in Erie County.

Here males of the first form were abundant. while those of the second form were few and small (between 32 and 43 mm. long). The latter consequently all belonged to the generation of that year. Some of them very likely would have changed into the first form within a short time. The smallest male of the first form was 39 mm. long.

In addition I have seen specimens from Lake Erie, Lorain County, Ohio (Oberlin Museum) collected May 1, 1892, which demonstrate the presence of males of the first form in spring, and I have received from Mr. E. B. Williamson a couple collected September 1, 1904, in Emmet County, Michigan, in the act of copulation. The date is slightly ahead of my earliest date for this act in *C. obscurus*, but falls into the same general season. All these dates perfectly agree with the rules laid down for *C. obscurus.*

Of *C. propinquus sanborni* I have collected material only in the early spring and late summer. The specimens observed in spring (April 14 and 28, 1905), in the Tuscarawas drainage, Ohio, correspond entirely to the spring condition of *C. obscurus.* Generally they have a thick coat of dirt, showing that they have gone through the winter without moulting. Most of the males are of the first form, but a few are of the second form, and these have new shells. A large number of the females have eggs. From Dr. Sterki I received a number of newly hatched young, 12–15 mm. long, collected on June 18, 1906, at Dennison, Tuscarawas County, Ohio. Among the specimens collected on August 28 and 29, 1905, in Wetzel and Pleasants Counties, West Virginia, many males of the first form were present, but also a considerable number of the second form; besides, there were a number of small specimens of the generation of that year. Among the material of this form from Oberlin, collected September 28, 1903, the same was true, and thus in this form also the known facts agree with what has been observed in the case of *C. obscurus.*

3. *Cambarus limosus.*

This is the species on which Andrews (1895 and 1904) made his observations. My own dates, which are supplemented by those collected by Mr. H. Gera and Mr. W. R. McConnell, are comparatively few, but, as far as they go, show certain discrepancies with Andrews' results, which need attention and explanation.

The largest number of observations I possess are dated in the month of September, when I collected this species at numerous localities in eastern Pennsylvania, New Jersey, and eastern West Virginia in the years 1898, 1904, and 1905. At this time the condition of this species entirely corresponds to that of *C. obscurus.* Males of the first form are abundant and of all sizes. (Smallest, 37 mm. long, from Stony Brook, Princeton, New Jersey, September 21, 1898, and 40 mm. long, from Grenoble, Bucks County, Pennsylvania, September 20, 1904.) Males of the second form are scarce, and most of them are of small size (between 28.5 and 40 mm. long). Among the females also are many small individuals (as small as 25 mm. long). These small specimens clearly belong to the youngest generation, born in the spring of the year of capture.

Copulation was observed by Mr. H. Gera on September 4, 1905. I saw a repeated copulation of the identical couple on September 10, 1905, and again, in other specimens sent to me alive by Mr. Gera, on November 4, 1905. In addition I have seen this species copulating in captivity in the Anatomical Laboratory of Princeton University in January, 1899, (Ortmann, 1900, p. 1242). Thus the copulating season is identical with that of *C. obscurus*, and lasts from September into the winter, possibly January.

C. limosus goes through the winter,[74] and is found in spring in the same condition as in fall (April, 1899, at Princeton). In May I found females with eggs (May 9, 1905, Potomac River, Cumberland, Maryland), and on May 30, 1898, I collected females with young under the abdomen (Stony Brook, Princeton, New Jersey). Thus the spawning season seems to be identical with that of *C. obscurus*. During a part of the summer males of the first form seem to be absent. I record that in July, 1904 (specimens collected by H. Gera in Camden County, New Jersey, without exact date), no males of the first form were found. In a large set preserved in the Academy of Natural Sciences of Philadelphia, collected by H. W. Fowler in the Delaware River at Holmesburg, Philadelphia County, on July 4, 1899, all the males are of the second form, and this although there are specimens in this set over 80 mm. long. Among the collections of W. R. McConnell there is a set of this species taken on July 10, 1905, at Milesburg, Center County, which contains two males of the first form, with quite fresh shells. This date corresponds closely to the first date (July 11), at which males of the first form of *C. obscurus* were observed.[75]

According to the above records it seems very likely that the seasonal history agrees in every particular with that of *C. obscurus*. The mating season in fall, the spawning season in spring, and the absence of males of the first form in early summer (June and part of July) agrees with what we know of *C. obscurus*. Comparing this with the account given by Andrews, we find the following differences.

---

[74] I collected specimens in January, 1899, in the Delaware-Raritan Canal, near Princeton, New Jersey. All the males were of the first form. Collecting was done by seining under the ice. The crawfishes were obtained in water about four or five feet deep.

[75] Mr. McConnell collected a newly moulted male with a soft shell, of the first form, at Bloomsburg, Columbia County, on July 19, 1905, and during August he has several dates for these males: August 10 (Reading); August 18 (Marion); August 21 (Greenpark); August 22 (Landisburg).

Andrews (1904, p. 166) places the normal mating season in the months of February, March, and the beginning of April, and says that there seems to be an autumnal pairing (October, November) "in place of or in addition to" the spring pairing. I believe, however, that the autumnal pairing is the normal one, which may be extended through the winter. Indeed I have observed it in January, but only in specimens kept in captivity. Since Andrews' observations were made in the laboratory, it appears probable that the mating may be continued or repeated under exceptional conditions such as are offered in captivity, but that this is not normal. In *C. obscurus* I am positive that under natural conditions copulation does not take place in March and April.

The time of spawning, as observed by Andrews (1904, p. 176) agrees well with our records (end of March and April), also the time of hatching (*l. c.*, p. 187), late in May.

As to sexual maturity, Andrews did not gather facts to show that females are mature and oviposit at the end of the first year (1904, p. 206), although he observed copulation at the end of the first summer. I observed, on November 4, 1905, copulation taking place in specimens less than 45 mm. long, and found females "in berry" of the size of 50 and 45 mm. (Cumberland, May 9, 1905). Since the same fact has been observed in the case of *C. obscurus* it is certain that males as well as females are sexually mature at the end of the first summer, and that the sexual union is effective, the females spawning the following spring. However, in such small females the number of eggs is generally very small (fifty or less).

Thus it seems that *C. limosus* agrees perfectly with *C. obscurus* in its life-history, and that the only marked difference from Andrews' account concerns the mating season. This is however apparently due to the fact that Andrews' observations were made in the laboratory. The explanation for this is very likely to be sought in the temperature conditions. The water used in tanks in laboratories has generally a rather uniform temperature throughout the year, while under natural conditions the temperature of ponds, rivers, and streams varies considerably in summer and winter. I made a few observations with reference to *C. obscurus.* In January, under the ice, the water is near the freezing point, say about 35° F.; on April 6, when females were found spawning, the temperature of Thorn Creek, Butler County, was 45° F. On May 1 the temperature of Grave Creek, Marshall County, West Virginia, was 66° F. and spring moulting was going on. In midsummer I observed a temperature of 82° F. in Bates Fork, Greene County, on July 24, and a temperature of 78° F. in the Ohio, at Ambridge in Beaver County on August 24.

This gives a range of from about 35 to 80 during the year, and I have no doubt that the nice restriction of certain periods in the seasonal history is primarily due to differences of temperature. It is only natural that an equalizing of the temperature must tend to efface the seasonal periods.

4. *Cambarus diogenes.*

According to my observations, which extend over the period from March 22 to November 17, this species also agrees in the main features of its seasonal development with *C. obscurus.*

I have the following records for females with eggs: April 6, 1905; April 19, 1905; May 2, 1904; May 14, 1899, (collected by Atkinson, Graf, and Williamson); May 21, 1906; May 22, 1905; May 27, 1904. On May 21, 1906, and June 2, 1905, I found several females with newly hatched young under the abdomen. In no other part of the year has this been observed, and thus the spawning and hatching season is well fixed (April, May, and the beginning of June), and is found to be identical with that of *C. obscurus.*

The number of eggs is considerably less than in the case of *C. obscurus,* and generally falls considerably short of one hundred. The spawning does not take place outside of the burrows, but inside of them, and this was most evident in a female collected on April 6, 1905, (Renfrew, Butler County), in which the eggs were quite fresh, with traces of the "apron" still visible. This female was dug out of its hole, as were all the rest with eggs or young ones.

After hatching the young remain a short time under the abdomen of the mother. But soon they leave her, yet remain in the same hole. I have repeatedly found young specimens in the same hole with their mother, namely, on June 13, 1904; June 15, 1905; July 6, 1905; July 19, 1905. The smallest were about 10 mm. long. These young specimens generally occupy a separate part of the burrow, and are often found near to and inside of the mouth of a closed chimney. They remain in the hole until they attain a length of 20 mm., which happens toward the end of July. Then they leave the hole of the parent crawfish and begin to build their own little holes and chimneys. I observed this on July 26, 1904, at Derry, Westmoreland County, when I discovered a female 20.5 mm. long in a small hole of its own. At the same date I found a larger one, 30.5 mm. long, which may have belonged to the same generation. On August 4, 1904, at Francis Mine, near Burgettstown, Washington County, I found numerous young specimens between 20 and 29.5 mm. long, all in their own holes. On August 22, 1905, at Squaw Run, Allegheny County, I discovered two young specimens 22 and 28 mm. long. On August 26, 1905, at Baden, Beaver County, specimens 31.5 to 42 mm. long were found apparently under the same conditions. As late as September 5, 1904, (Smithfield, Fayette County), and October 6, 1905, (Kittanning, Armstrong County), I found two very small specimens (24 and 20.5 mm. long) in small holes. Never after July 19 have I found young ones in the hole of the mother, so that it is quite sure that at the end of July they invariably shift for themselves when they have attained a length of about 20 mm. The largest found in the hole with its mother was 18.5 mm. in length, on July 19, 1905. Since young specimens found in the same hole, apparently being brothers and sisters, often have a different length (15 to 18.5 mm. in the case just mentioned), and since, as said above, specimens of only 20.5 mm. in length are found as late as October, the rule is established in the case of this species also that the individuals of the same litter grow up at a different rate.

With regard to the presence of males of the first form, the same conditions seem to prevail as in the case of *C. obscurus.* These males are frequent in spring. I found them at the following dates: March 23; April 2, 6, 15, 16, 24, 30; May 2, 3, 13, 14, 21, 22, 27, 29; June 2, 15. Then follows a gap of over a month to July 20. Within this period I made observations upon the following dates: June 16, 18, 26, 27; July 6, 16. At none of these dates did I discover a male of the first form. It is true that the material in this species is less abundant, a dozen specimens collected on one day representing a rich haul; but it is nevertheless remarkable that during the period just mentioned, in which particular pains were taken to get males of the first form, none were secured. But after this they again appeared regularly, namely: on July 20; August 7, 8, 22, 26; September 5, 7, 15, 19, 21; October 6, 9, 11, 18, 24; November 5. This makes it evident that in early summer (end of June and beginning of July) there is a time when no males of the first form are present.

However, males of the second form are found at any time in the year as frequently as those of the first form. In this respect *C. diogenes* seems to differ from *C. obscurus.* This seems to be due to the fact that *C. diogenes* attains sexual maturity at a later age than *C. obscurus* and the river species in general. The smallest male of the first form ever found measures 55 mm. in length (August 22, 1905, Montrose). It is hardly possible that this individual should belong to the generation born in June of the same year, since the latter are known to be at that time about 30 or at the utmost 40 mm. long. We may assume that *C. diogenes,* like *C. obscurus* and *C. limosus,* may attain at the end of the first summer a length of about 40 or 50 mm., but these individuals do not then assume the first form as the river species do. The same is true of the females. The smallest seen in copulation (or associated with a male) was 63 mm. long, and the smallest female with eggs was 62 mm. long.

Young specimens less than 30 mm. long have not been found in spring, with one exception, when a female of 25.5 mm. in length was found on May 27, 1904, at Squaw Run. This, however, apparently was an exceptionally delayed individual of the generation of the previous year. It was found under unusual conditions, under a stone on the banks of the creek, evidently removed from its original habitation by winter or spring floods. No additional specimens were seen in close proximity.

I cannot say much in the case of *C. diogenes* in reference to the regular moulting periods which were observed in *C. obscurus* to take place in spring and fall. I have repeatedly found soft shells, and on April 24, 1904 (Nine-Mile Run, Pittsburgh), at a place where a large colony of this species was present, I picked up numerous cast-off claws,[76] which would indicate an early spring moult. But these claws may have accumulated during winter and spring. The rate of increase at a moult was measured in one instance. A female, 52 mm. long, captured on April 6, 1905, was kept in captivity, and moulted on July 16. After this process it was 54 mm. long. This cannot be regarded as entirely normal, since the specimen was kept under unfavorable and artificial conditions.

The copulating season of this species also falls in the autumn. I have only twice observed a male and female in copulating attitude, but in both cases they let go when disturbed. This was on November 5, 1904 (Nine-mile Run, Pittsburgh), and on October 24, 1905 (Branchton, Butler County). The first couple was found in water inside and near the mouth of a comparatively simple hole. The male was 70 mm., the female 81 mm. long. The second couple was found a little deeper, but not over a foot, also in water. The male was 64 mm., the female 63 mm. long. Mr. F. E. Kelly reports a similar observation made by him on November 14, 1904. Besides on two other occasions I found males and females associated in couples in the same hole. Three cases were observed on September 5, 1904, at Smithfield, Fayette County, and two cases on August 26, 1905, at Baden, Beaver County. Since it is an absolute rule that under ordinary circumstances only one specimen occupies a hole, these finds are significant, and, inasmuch as in all these cases it was always a male of the first form which was associated with a female of good size (over 63 mm. long), it is evident that this association was connected with the mating process. Whether the male visits the female, or *vice versa*, I do not know. In every case the pair was easily captured, being lodged not far from the entrance of the hole. In some of these cases I was struck by the simple character and small depth of the burrow, and it may be that the couples dig out small, temporary holes for the mating time. This, however, needs further investigation, and possibly, if found to be the case, may, nevertheless, not be the general rule.

---

[76] After moulting the shell is generally eaten up, with the exception of the big claws.

In no other part of the year were similar observations made, and this fixes the mating season for the months of August, September, October, and November,[77] agreeing with what we have observed in the case of *C. obscurus.*

Thus we see that the seasonal cycle in the life of *C. diogenes* corresponds closely to that of the river-species. The only difference is in the time when sexual maturity is reached, and it seems that in the case of *C. diogenes* this does not occur earlier than at the end of the second summer. Whether this influences the duration of life is not known. Nevertheless the fact that this species frequently, or even regularly, reaches a size superior to that of *C. obscurus*, specimens of over 90 mm. in length being quite often found, suggests that this crawfish may live more than three years, possibly four or five.

The resemblance of the life-history of this burrowing form to that of the river species is due, I believe, in large part to the similarity of conditions of temperature. As has been stated, *C. diogenes* lives near stagnant water and swamps, in places where there is generally not much fresh and cool water, although such places are not strictly avoided, and where the temperature of the water is subject to considerable seasonal changes. In winter and spring the water in the holes is rather cool (43° Fahr. on March 23, 1905, in Nine-Mile Run), while in midsummer it becomes when stagnant, almost lukewarm.

The above observations are in part at variance with those made by previous writers on the same species. Girard (1852, p. 88), near Washington, D. C., found females with eggs in March and April, which agrees with our dates, making allowance for the difference of climate between Washington and western Pennsylvania. Girard also noticed the fact that as a rule only one individual was found in each hole and mentions as an exception that in one burrow a male and a female were found together. However, he neglects to tell the exact date of this find (his observations were chiefly made in spring). In one case, he says that a male was seen walking over the surface of the ground, as he believes, in search of the female. But in this instance also no date is given.

Tarr (1884, p. 127) never found male and female together (in May, near Washington), and always only one individual in each burrow, and he never found specimens outside of the holes.[78] He further believes that the burrowing crawfishes retreat to the streams in the winter, and in spring construct holes for the purpose of rearing their young, and that impregnation takes place after the winter has passed. These ideas are not supported by any evidence, and are, as we have seen above, incorrect. His opinion that the same burrow is not occupied for more than one year is also not supported by our observations. The time of hatching of the eggs is given as about the middle of May (p. 128), which agrees with our dates. Faxon (1885a, p. 74) reports that according to Mr. P. R. Uhler the female during the period of incubation goes into pools, ditches, etc. This, however, is contrary to the observations of Girard, Tarr, and myself. All these particulars refer to the eastern form of *C. diogenes*, on the coastal plain, and it seems that with regard to the spawning season and the spawning habits this form agrees with that of western Pennsylvania, always considering the slight difference in climate which makes this season begin a little earlier in the Atlantic lowlands.

---

[77] It possibly extends further into the winter, as in the case of the other species discussed.

[78] Although I have myself never seen a specimen of *C. diogenes* walking over the ground, this must sometimes occur, for males and females must come together in the mating season, and the holes do not communicate underground. According to Williamson (1901, p. 12), *C. diogenes* and *C. monongalensis* are nocturnal, and that they come out of their holes at night is shown by the fact that Mr. Rhoads captured some of them in traps set out over night for rodents.

The observations made on the western form show more marked differences. Bundy (1877, p. 171) reports the discovery of a female with eggs nearly ready to hatch, near Mechanicsburg, Henry County, Indiana, on January 1, 1875. Hay (1896, p. 491) found that the breeding season in Indiana is in early spring, and observed copulation on April 2, 1892. At this time the specimens leave their burrows, and are frequently found in open ditches and streams. The eggs were laid from April 18 to April 30. He also repeatedly saw females with well grown young in small streams. According to Harris (1890, p. 267) a female with eggs was found in Kansas on May 3, 1891,[79] apparently in an open ditch, as is shown by the subsequent sentences.

With the exception of Bundy's record these dates show April and May to be the normal spawning season of the western form also. The observations of Hay and Harris, that *C. diogenes* frequents open ditches in spring, and that it copulates in spring, are, however, entirely at variance with the habits of this species in western Pennsylvania. This is not the case here, and I have never seen specimens outside of their holes in spring. My observations began as early as March 23, at a time when the frost was hardly out of the ground.

That this is also not the general rule in northern Indiana is shown by notes sent to me by Mr. E. B. Williamson from Bluffton, Wells County, Indiana. Mr. Williamson writes to me: "As to *C. diogenes* congregating in ditches and the like in spring I have no evidence here. The large males of *diogenes* can be expected in almost every little stream. They move about on the bottom restlessly, not lying concealed. Often the current catches them and they roll over and over, but they always keep moving. *Diogenes* also wanders across country at this time, in daylight as well as at night. I have found several crushed in wagon roads. *Under these circumstances I have yet to find a female.*" In another letter Mr. Williamson says pertinently that the specimens taken by him in spring in open ditches are all old males, "in which the death instinct had developed."

---

[79] *Sic.* Note the discrepancy between this date and the date of publication.

Thus it seems evident that the western form does not agree with the form found in Pennsylvania in so far that in early spring the specimens seem to habitually leave their holes. Whether it is only old males when about to die (analogous to what we observed in the case of *C. obscurus*) which wander about, or whether the females with eggs also are found in open water, and further, whether copulation normally takes place in spring, are assumptions which remain to be proved. The observations of Bundy, Hay, and Harris are surely correct, but it remains to be ascertained whether they represent exceptional cases, or whether they are the rule. Moreover it is not improbable that in the western form the seasonal cycle is slightly different, since it lives under somewhat different surroundings. Hay (1896, p. 491) reports that during the dry months of the summer *C. diogenes* seems to lie at the end of the burrow (which contains hardly any water) in a sort of a stupor. I never observed anything like this in Pennsylvania, the holes of *C. diogenes* being always well filled with water at the bottom, and the crawfishes being very lively.

That observations on the habits of this species should always be considered carefully with reference to all accompanying facts is evident from the following case: Dr. D. A. Atkinson found a number of specimens on April 20, 1905, in open pools near Westview, Allegheny County, Pennsylvania, in a region where this species is abundant. These pools were in the course of an old, abandoned mill-race, which dried out late in summer. All these specimens, seven in number, were young, measuring from 33 to 52 mm. in length, and consequently belonging to the generation of the previous year. Now, bearing in mind the fact that the late summer and fall of 1904 and also the winter of 1904–5 were characterized in our region by an extreme lack of precipitation so that all streams were exceptionally low till the middle of March, 1905, when a flood (March 20 to 25) restored the normal conditions, it is very likely that this mill-race was dry in the summer and fall of 1904, when these young specimens began to make their own burrows. They selected this place as a favorable one, and remained there all through the winter, a few smaller floods, one on January 13 and another on March 9, not disturbing them, till the big flood filled the mill-race again for a longer time, Such conditions, however, do not suit this species, and consequently the specimens came out of their holes, and were found, at least for a time, in the open pools, till they had selected more convenient locations in the neighborhood. Thus this case must be regarded as exceptional, not as a regular or normal episode in the life of the species.

5. *Cambarus bartoni and Cambarus bartoni robustus.*

In all the species discussed so far we have found a regular seasonal period in the life-history, marked chiefly by a distinct mating-season in fall, a spawning-season in spring, and a season in early summer when no males of the first form are present. But it is entirely different in the case of *C. bartoni.* In this species none of these seasons is recognizable.

As to the mating period, I have observations on only two dates. On May 27, 1904, I found a couple *in copula* in Squaw Run. Here I was able to make a close observation. The act of copulation is similar to that in the case of *C. limosus*, as described by Andrews (1904), but the male does not take hold of the anterior walking feet of the female with its chelæ, and its second pereiopods are clasped around the carapace of the latter, lying in the cervical groove, and almost touching each other on the back of the female. In this case it was the fifth pereiopod of the left side, which was stretched across the sternum in order to elevate the copulatory organs. The male of this couple was 67 mm. long, the female 73 mm. long. The other observation occurred on October 6, 1905, when I found two couples together at Weskit, near Kittanning. The male of the first couple was 63.5 mm., the female 59 mm. long. In the other couple both male and female were 63 mm. long. Both couples separated when captured, and thus I cannot give particulars.

These two dates are so far remote from each other that it seems hardly probable that they belong to one and the same breeding season. It is possible that one of them is exceptional, but I have no means of deciding this. On the other hand, as we shall see presently, spawning takes place at such different times of the year that very likely the mating-season is also irregular.

Females with eggs have been found on the following dates: July 6, 1905; July 10, 1905; July 20, 1904; July 29, 1905; August 1, 1905; August 9, 1904; August 10, 1905. The number of eggs was between seven and one hundred and thirty-three, the smallest number being found in the smallest individual, 59 mm. long. In addition I took a number of females with young under the abdomen. The following records are at hand. At Princeton, New Jersey, in February, 1898. The exact date is not recorded, but it was toward the end of the month. The length of the female was 48 mm., the number of the young was ten.[80] Further: March 31, 1905;

---

[80] This number is unreliable, but represents as many as were secured. In some cases quite a number of the young dropped off when the mother was captured.

length of mother 71 mm., ten young; August 18, 1904, length 59 mm., ninety-two young; September, 20, 1905, two cases, one 53 mm., long, with thirty-nine young, and another 55 mm. long, with thirty-five young; November 8, 1905, 73 mm. long, with one hundred and eleven young; November 22, 1905, two cases, one 84 mm. long, with seventy-five young, and another 67 mm. long, with sixty-eight young.

This extends the spawning season over the following months: February, March, July, August, September to November. Since young were found in February and November, these must have been in the egg-stage at least a month before they were captured, and this would add January and October. Thus we have only interruptions in December and from April to June. The gap in December may easily be filled, and be due only to the incompleteness of our investigations in winter, but the gap in April, May, and June may be real.

If there is any spawning-season in *C. bartoni* it would cover nine months of the year, from July to March. This, however, is entirely different from what we have seen in the river species, where the spawning season falls exactly in the months where no spawning has been odserved in *C. bartoni*. And besides, this gap may be partly filled in *C. bartoni*, for I have found very young specimens (between 10 and 20 mm. long; the newly hatched young are 9 to 11 mm. long) on the following dates: May 16, 1905 (13 to 14 mm.); May 25, 1905 (11 mm.); June 2, 1905 (about 17 mm.); June 12, 1905 (14 mm.); June 17, 1905 (15 mm.); August 22, 1905 (10 to 11 mm.).

The conclusion is that very likely *C. bartoni* has no defined spawning-season, but may spawn at any time of the year, and that accordingly the mating-season is also not restricted to a particular part of the year. The latter is further substantiated by the fact that males of the first form are found practically all the year round. I have the following dates: March 21, 28; April 19; May 7, 9, 17, 21, 25, 27, 30; June 2, 3, 6, 12, 13, 16, 23, 24; July 10, 12, 18, 26, 29; August 1, 10, 18, 22, 26; September 11, 16, 20, 21, 30; October 5, 6, 10, 12, 17, 24, 31; November 8, 22; December 25. The only two months missing are January and February, when no collecting was done. On the other hand males of the second form are also abundant all the year round, and were found, with the exception of January and February, in every month.

Under these circumstances it is impossible to say anything about the life-cycle of the single individual, since different generations cannot be traced. But one thing should be mentioned. The males of this species do not seem to attain sexual maturity as early as the river-species. The smallest male of the first form ever found in eastern Pennsylvania is 49 mm. long, and in western Pennsylvania 50 mm. long. The smallest female with eggs or young is from New Jersey (Princeton), and is 48 mm. long. From the eastern part of our state I have seen none smaller than 55 mm. long, and in the western part the minimum is 59 mm. in length. This is considerably above the minimum size of sexually mature specimens of *C. obscurus* and agrees better with *C. diogenes.*

In one case I have been able to observe the increase in size which takes place upon moulting. On July 11, 1905, I found at Tionesta, Forest County, a female in the act of shedding, and succeeded in keeping her alive till the new shell was hard enough to be measured. The old shell was 32 mm. long, and the new one 36 mm. in length. In this case the crawfish withdrew from the old shell through a crack that appeared on the dorsal side between the carapace and the abdomen.

We have seen above that the regular seasonal cycle observed in the river-species is probably due to the regular and considerable changes of temperature taking place in the rivers. *C. bartoni* lives in small streams, which generally are much cooler in summer than the larger ones, and this apparently explains the difference in the seasonal history. The temperature conditions under which *C. bartoni* is found, are more uniform throughout the year, and consequently no regular seasonal periods in the life are observed.

No previous observations on this species have been published, except Williamson's note (1899, p. 47), that this species was found with young under the abdomen on March 28, 1899, at Columbus, Ohio. This lack of information is rather singular, considering the extreme abundance of this form in the eastern part of the country.

Cambarus bartoni robustus very likely is identical in its life-history with the typical form. I have made observations at only a limited number of dates, but they tend to show that there are no marked seasonal periods.

The following dates for the capture of males of the first form are at hand: May 27, 1904; July 11, 1905; August 22, 1905; September 18, 1900 (Atkinson collection); September 30, 1905; October 4, 1904; October 6, 1904; November 14, 1903 (Mus. Oberlin). The smallest male of the first form measures 63 mm. in length.

Males of the second form were taken in the months of May, June, July, August, September, and October. They were abundant in every case, considering the number of specimens secured.

Copulation was never observed. A female with eggs was found on July 11, 1905, at Spartansburg, Crawford County. It was 84 mm. long, and the number of eggs was 228, more than twice the number of those usually observed in the typical *C. bartoni.* Young specimens, less than 20 mm. long, were taken on May 27, 1904 (18 mm.); and were numerous in a lot collected by Miss G. Kinzer on August 27, 1905 (9 to 16 mm.).

For the months of December, January, February, March, and April, no records are at hand.

6. *Cambarus monongalensis and Cambarus carolinus.*

The temperature conditions under which these two species are found are similar to those observed in the case of *C. bartoni*, and they are even more uniform, considering the fact that both are exclusively restricted to spring-water, avoiding even small streams. In 1905 I took the following measurements of the temperature of the water in the holes of *C. monongalensis* (May 16 at Morgantown, the rest at Edgewood Park); March 18 (ground still frozen in places); 39° F.; May 16, 58° F.; July 8, 63° F.; August 18, 68° F. The range is considerably less than that given for *C. obscurus* (35° to 80° F., see above, p. 479). We consequently should expect a similar irregularity in the seasonal history as in *C. bartoni*, differing markedly from the third chimney-builder, *C. diogenes*. This is indeed the case.

My observations are rather complete with reference to *C. monongalensis*, covering the time from March 18 to December 26. During no period within this time were males of the second form absent or scarce, but males of the first form were also almost regularly found; the following are the dates for the latter: March 18; April 4, 21, 24; May 1, 6, 9, 16, 21, 24; June 3, 30; July 6, 8, 20, 24; August 7, 13, 18; September 10; October 9, 10; November 8.

Copulation was not observed; but in one case, May 6, 1904, (Fern Hollow), a male of the first form and a female (55 and 72 mm. long respectively) were found together in the same hole. The smallest male of the first form ever found was 53 mm. long.

Females with eggs were obtained on June 25, 1906 (O. T. Cruikshank); June 28, 1905, (three specimens); June 30, 1904, and July 20, 1905. These few observations would tend to restrict the spawning-season to the months of June and July, but this conclusion is not admissible, since newly born young are found at various other parts of the year. I have such (less than 20 mm. long) taken from the hole of the mother, at the following dates: April 4, 1905 (13 mm. long); April 29, 1905 (18 mm. long); May 1, 1905 (17 to 20 mm. long); May 2, 1905 (16 to 21 mm. long); May 6, 1904 (19 mm. long); June 11, 1904 (19 to 20 mm. long); August 18, 1905 (14 mm. long); September 24, 1898 (19 mm. long and above, collected by Rhoads and Williamson); October 29, 1904 (19 mm. long). This extends the spawning-season considerably, but it has the appearance of being interrupted during the winter.

The smallest female with eggs is 58.5 mm. long. The number of eggs is between thirty-eight and seventy-nine, which is considerably less than in the river species, and also on the average slightly less than in *C. bartoni* and *diogenes*.

In this species the young of one litter seem likewise to grow at a different rate. Thirteen young found with the mother in the same hole on May 2, 1905, were between 16 and 21 mm. long. Ten young found on June 16, 1904, were from 20.5 to 32.5 mm. long. Twenty-two young, found on July 20, were from 22 to 27 mm. long. Twenty-four specimens dug out with the mother by Rhoads and Williamson[81] on September 24, 1898, are from 19 to 29.5 mm. long.

Thus it seems that *C. monongalensis* agrees well with *C. bartoni.* No well-marked spawning-season is present. At any rate the spawning-season extends over a very large part of the year, and, correspondingly, no well-marked mating-season can be distinguished. Males of the first form may be found at any time, and also males of the second form. Sexual maturity is delayed, males turning into the first form comparatively late, and the females also are not mature before they have reached a larger size than the river species. In all these respects, except sexual maturity, *C. monongalensis* differs from *C. diogenes.*

There are further differences from *C. diogenes* in the development of the young. We have seen that young *C. diogenes* remain in the hole of the mother for some time after they have left the abdomen of the latter. When hatched they are about 9 or 10 mm. long, and leave the mother very soon, since free individuals have been found only 10 mm. long. When they have grown to about 20 mm. in length, they leave the hole of the mother.

In *C. monongalensis,* however, they stay considerably longer in the hole of the mother. The exact time cannot be ascertained, but we can draw conclusions from their size. Free young specimens from 13 to 25 mm. in length are always found with the mother. The smallest specimen which had begun to make a hole of its own was 26 mm. long (August 7, 1905, Fern Hollow). Another was 29 mm. long (October 28, 1905, Edgewood Park). Specimens over 30 mm. long generally have built their own burrows. But there are exceptions. As we have seen, young up to 32.5 mm. long have been found with the mother; and further, on July 24, 1905 (Deer Lick), I took out of one hole fifteen young, measuring from 27 to 33 mm. in length, and out of another hole three young measuring 37, 39.5, and 40 mm. in length. In these cases the mother was also in the hole. Although in the last two cases conditions seem rather abnormal, it is certain that the young of *C. monongalensis* remain longer in the hole of the mother than those of *C. diogenes.* While the latter begin to shift for themselves when about 20 mm. long, young specimens of *C. monongalensis* do not do so before they reach 25 or 30 mm. in length, and may even postpone this step till they have attained a larger size (maximum 40 mm.).

---

[81] Williamson (1901, p. 12) says that there were forty-seven young ones: only twenty-four are now in the collection of the Carnegie Museum (Cat. No. 74. 25). Possibly this discrepancy is due to a misprint.

I once observed the change of a male from the second form to the first form. The specimen was 58 mm. long, and was dug out of its hole on August 18, 1905, at the type locality, Edgewood Park. It was kept in a jar in water, and had moulted on August 30. I had been away on an excursion on the two preceding days, but on August 27 it had not yet shed. When the fact was discovered it had eaten the larger part of its old shell, only the claws remaining, which were also eaten up subsequently, all but the finger-tips, by September 4. The new shell measured 61 mm. in length. When captured this specimen was of the second form. After moulting it was of the first form.

On account of the irregular spawning season it is impossible to trace the life-history of one and the same individual, and consequently we cannot draw conclusions as to the duration of life.

The few observations on *C. carolinus* entirely agree with those made on *C. monongalensis.*

Males of the second forms were found in May, June, July, August, and September. For males of the first form I have the following dates: May 17, 1905; June 24, 1904; August 2, 1905; August 11, 1904; August 12, 1904; September 5, 1905; September 7, 1904; October 16, 1905. The smallest male of the first form measures 56 mm. in length.

Two females with eggs were secured on July 12, 1904. One was 80 mm. long, and had only three eggs; the other was 77.5 mm. long, and had seven eggs. These numbers seem strangely small, and apparently are not normal, for on August 1, 1905, I found a female 69.5 mm. long, with twenty-two young under the abdomen. But even this number is below the average of *C. monongalensis.* While these cases seem to indicate a spawning season in July, the finding of very young ones in the hole of the mother at other dates considerably extends this period. I have found such on May 17, 1905 (17 to 21 mm. long); June 13, 1905 (14.5 to 21 mm. long); August 1, 1905 (18 to 23 mm. long); August 2, 1905 (28 mm. long); August 9, 1904 (17 to 25 mm. long); August 11, 1904 (19 to 29 mm. long).

The largest young remaining with the mother were 29 mm. long, while the smallest in a hole by itself was 30.5 mm. long. Thus the time of leaving the hole of the mother is about the same as in *C. monongalensis.*

The above observations are not at all sufficient to show that *C. carolinus* agrees entirely with *C. monongalensis,* but since both species are alike in so many particulars, morphological and ecological, and since the above dates do not show any differences, we may safely assume that the life-history of both species is similar.

The seasonal history is rather well known in four of the species above discussed, *C. obscurus*, *C. bartoni*, *C. monongalensis*, and *C. diogenes.* These are the species found in Allegheny County, and they are most complete, since I had the best chance to study them, three of them being found in the immediate vicinity of my residence and the fourth (*obscurus*) within a few miles and within easy reach.

We are able to distinguish two main types of life-history, which I should like to call for convenience the *warm water* and the *cool water types.* *C. obscurus* and *diogenes* represent the first, and agree with each other in having well marked mating- and spawning-seasons, and in early summer a period when no males of the first form are found. They differ, however, in the fact that in *C. obscurus* sexual maturity is reached, as a rule, at the end of the first summer, which does not seem to be the case in *C. diogenes.* Of the other species, of which no complete series of dates are at hand, the river-species, *C. limosus*, *C. propinquus*, and *C. propinquus sanborni*, very likely agree with *C. obscurus*, for the comparison of the dates does not reveal any differences.

The *cool water type* is represented by *C. bartoni* and *C. monongalensis.* Both are characterized by the absence of well marked mating- and spawning-seasons. They may be expected in any stage of development at any part of the year, even winter making no exception. *C. carolinus* probably belongs also to this type, although the observations are too scanty to positively establish the fact.

One thing in conclusion should be especially emphasized. The life-history and the habits of different species of the genus *Cambarus* are by no means similar. On the contrary they differ considerably, and the differences may be accounted for primarily by the different ecological conditions under which they live. Consequently it is inadmissible to generalize from facts observed in one species only, and further it is to be expected, if other species are studied, that additional types of life-history will be discovered.

VI. ECONOMIC VALUE.

1. *Popular knowledge of Crawfishes.*

The crawfishes of this state are generally well known to the population. They are abundant and large enough to attract the attention even of the casual observer. But it is chiefly the small boy who is interested in them. Three popular names are employed for them, *crab*, *crayfish*, and *crawfish.* "Crab" obviously is a misnomer, belonging originally to the marine *Brachyura*, but it is largely in use all over the state, and chiefly so in the cities. The word "crayfish" is used the least. In my experience I heard it mostly in the mouths of such people as had a certain amount of schooling and had acquired some knowledge of natural history. This word is preferred by teachers generally, very likely in consequence of its use in one of the standard works on these creatures (Huxley, "The Crayfish"). The third word, "crawfish," is the proper American name. I found it commonly in use in the rural communities where "crayfish" and "crab" were often entirely unknown. This is chiefly the case in the southwestern section of the state and in West Virginia. In one or two cases in Fayette and Somerset Counties I heard a distinction made between "crab" and "crawfish." The former name was used for the river and brook forms, *C. obscurus* and *C. bartoni*, the other for the chimney-builders. All three words go back to the same root, Old German *krebis*, from which is derived on the one hand the modern German *Krebs*, and the English *crab*; on the other hand the French *écrevisse*, the English *crayfish*, and the American *crawfish*. The latter form, being typically American, and being exclusively known to the natives of a large part of the country (the farmers), I have decided to use it in preference to the other two forms.

In literature "crawfish" was used by Say (1817), Harlan (1835), Hagen (1870), Abbott (1873), Hay (1896). "Crayfish" was used by Abbott (1884 and 1885), Faxon (1885, 1890, 1898), Hay (1893, 1899), Andrews (1895, 1904), Shufeldt (1896), Osburn and Williamson (1898), Harris (1900), Williamson (1901, 1905). Thus "crawfish" has the priority.

Other names have been given incidentally. Rafinesque (1817) calls *C. limosus* "mud lobster," (I heard this name once in Delaware County). Say (1817) and Harlan (1835) call *C. bartoni* "freshwater lobster," and Williamson (1899) uses the abbreviation "cray."

2. *The use of crawfishes as food and bait.*

Although well known, crawfishes are not much used as food by the population of Pennsylvania; but this is generally the case in the United States. In some of the larger cities of the United States they are found more or less regularly on the market (see Ortmann, 1900, p. 1260), *C. limosus* being one of the species which is principally used for food. I have, however, never heard that this is the case in our own state, but it may be found in the markets of Philadelphia.[82]

Nevertheless crawfishes are eaten in this state, but not regularly. I have heard sometimes from boys that they had tried them, but only in "sport," and only exceptionally have I met persons who had eaten them repeatedly and were fond of them. Generally, this source of food is unknown to the masses in this state. Yet a dish of crawfishes is not to be despised. It is true, our species never attain the size of the highly esteemed European forms, but I know from my own experience that, as regards quality, the former are not inferior to the latter. Young specimens (and chiefly soft shells) may be fried in butter and eaten shell and all, while the abdominal muscles of older ones, when boiled in water, are very good.

---

[82] Rafinesque (1817, p. 42) says of *C. limosus* at Philadelphia, that it is "good to eat."

Of course, it is hard to create a taste for crawfishes among the masses, but I do believe that it would be worth while to try. Crawfishes are so abundant in certain parts of the larger rivers, *C. limosus* in the Delaware, and *C. obscurus* in the Ohio drainage, that it is easy to get any amount of them. It also would not be difficult to raise them, for instance in ponds, and to supply the market regularly and judiciously. And further, I do not see, why the "tails" (abdomen) could not be used for canning, exactly like the tails of shrimps and prawns.

Beyond this, crawfishes are used only as bait by fishermen. This use is quite general, and crawfishes form an important part of the fisherman's outfit especially in western Pennsylvania. They are most valuable in fishing for Black Bass (*Micropterus*), since these fishes seem to be very partial to this bait.

3. *Crawfishes as scavengers. Their food. Their enemies.*

The indirect economic value of crawfishes is best expressed by saying that they are scavengers, as decapod crustaceans in general. They dispose effectively and quickly of any decayed matter, animal or vegetable, coming within their reach. They also eat living creatures. This was known previously. Abbott (1873, p. 83) calls them (*C. limosus* and *bartoni*) "omnivorous," and "scavengers," and says that they eat water-weeds, and seize young Cyprinoid fishes. Andrews (1904, p. 175) fed *C. limosus* in the laboratory on raw and cooked meat, raw eggs, pieces of earthworms, and on *Chara* and *Hydrodictyon*. Williamson (1901, p. 12) reports that *C. monongalensis* was caught in traps baited with raisin and oatmeal. I used for my specimens in the laboratory all kinds of meat, and since I am especially fond of smoked sausage, I let them often partake of it when I had it for lunch. They also eat earthworms and green vegetable matter, for instance seedlings of several weeds (*Galinsoga*, and *Rumex acetosella*), grass, and water-weeds (*Vallisneria*). In nature they are often found at carcasses and other animal refuse lying in the water. They eat insects. For instance I have seen *C. bartoni* taking grasshoppers used as bait while fishing for trout (Tub Mill Run, Ross Furnace, Westmoreland County). In the case of the chimney-builders vegetable matter seems to be largely resorted to, not only fresh plants, but also decaying vegetation being used. In digging them out of their holes I repeatedly found masses of decaying leaves and the like lodged in some side branch of the hole in such a position that they could not have fallen in accidentally, but must have been brought in by the crawfish. In one case (October 9, 1905, Nine-Mile Run), I found in a side-pocket of a hole of a female *C. monongalensis* a number of ripe fruits of *Cratægus*, about a handful, which under no circumstances could have fallen into the position where they were found. The hole was under a large *Cratægus* bush.

Thus it seems that any vegetable or animal matter, either fresh, or decaying, serves as food for crawfishes, and although some species may prefer certain classes of food on account of taste or necessity, they all take readily to any kind, as is seen by the fact that in captivity they eat everything that is offered to them without discrimination. If nothing is given, they eat one another.

Crawfishes in turn serve as food for many animals, chiefly those which are aquatic. Among mammals we know that raccoons hunt for them. As has been mentioned above, birds eat them, and the kingfisher and other equatic birds do so quite regularly. The report of Audubon, (see Ortman, 1900, p. 1250), that the White Ibis captures the chimney-builders by throwing fragments of the chimney into the hole, and watching for the crawfish to come up, does not seem strange to me. At Ohiopyle I was told that a domesticated turkey kept upon the grounds of the hotel had the habit of watching the holes of *C. carolinus*, and that frequently he captured this species. I have myself seen this turkey standing motionless before a hole, but I did not observe the actual capture. I do not entertain the slightest doubt that this and other birds are able to catch crawfishes in this way, and do not think that it is necessary to drop dirt into the hole, since the crawfish comes up frequently on its own account, when it may be seized.

Crawfishes constitute an important part of the diet of certain snakes, more particularly of the water-snakes, *Natrix sipedon* and *leberis*. I have seen the latter disgorge *C. obscurus* when captured. (See also Atkinson, Ann. Carn. Mus., I. 1901, p. 149, 150.) On two occasions I have found garter snakes, *Eutænia sirtalis*, in holes of *C. monongalensis*; two specimens of this snake in one hole on October 18, 1904, (Fern Hollow), and one snake in a hole on October 28, 1905, (Edgewood Park). However, whether the snakes were after the crawfishes, or whether they simply were using the holes for winter quarters, remains doubtful.

Professor H. A. Surface writes to me that *Cryptobranchus allegheniensis* and *Necturus maculosus* are among the chief enemies of the crawfishes, and, indeed, these two salamanders are generally found at places where crawfishes abound. (Compare Eydeshymer, American Naturalist, XL, 1906, p. 128.)

They are, however, most valuable as food for the fish-fauna of our waters. As has been mentioned above, crawfishes are good bait for certain fishes, and it is very likely that many of our freshwater fishes depend largely upon crawfishes for nutriment. It would be interesting to investigate how far this mutual correlation between fishes and crawfishes holds good in our state. The presence of a river-species in our western streams, and its absence in any drainage systems in the central parts is very remarkable. Indeed *C. bartoni* is found in rivers, but only occasionally, and in small numbers. My own observations are not sufficient to give an approximate idea as to these relations, since I did not pay much attention to the fish-fauna, and the latter has decidedly deteriorated, at least in quantity, and the fish have become rather scarce in most of our streams. Possibly the decrease in the number of fishes has caused an increase in the number of crawfishes.

4. *Crawfishes as obnoxious creatures.*

For the river-species hardly a point can be mentioned which would tend to show that they are obnoxious to human interests, except the fact that they occasionally capture young fishes. It is different with the burrowing species, which often become troublesome. In regions where chimney-builders are abundant I have repeatedly heard complaints about the chimneys, and chiefly so in the case of *C. carolinus* in Somerset County, Pennsylvania, Garrett County, Maryland, and Preston County, West Virginia. Here the mud-piles may hamper farming operations by interfering with the harvesting machines, clogging and ruining them. At Selbysport, Maryland, I was told that conditions were so bad that the farmers tried to exterminate the crawfishes by throwing unslacked lime broadcast over the fields, which operation was partly successful, the crawfishes coming out of their holes by hundreds in a dying condition. I was told that this treatment, repeated several times, had considerably reduced the numbers of the red crawfish in this neighborhood. At no other place did I hear of attempts made to kill these crawfishes, although farmers were unanimous in denouncing them as a nuisance.

At a few places another complaint was made, namely, that the chimney-builders were cutting off and eating up sprouting crops. This was affirmed with reference to *C. carolinus* at Reedsville, Preston County, West Virginia, where a farmer told me that this species had cut off the largest part of a crop of buckwheat, so that practically nothing was harvested. At Parson, Tucker County, West Virginia, complaints were made that the same species had damaged sprouting corn; and at New Martinsville, Wetzel County, West Virginia, I heard that *C. diogenes* was charged with eating up all kinds of sprouting crops, corn and beans being especially named.

I do not doubt that these complaints are justified, and that the burrowing species actually eat and damage crops to a considerable degree. As I have observed, in captivity *C. monongalensis* and *C. diogenes* eat young plants, and they surely do so when not in captivity, young sprouting corn, buckwheat, etc., being rather succulent and attractive to them. If sown in a place where crawfishes abound these crops will surely be attacked.

This being the case, and besides the chimneys being also a nuisance, it might be desirable to exterminate the crawfishes in a given locality, or at any rate to reduce their numbers. For this purpose unslacked lime, the means employed by the farmers at Selbysport, might be used. But I am in no position to vouch for the efficiency of this remedy, having no personal experience (with the exception of the one case mentioned above, p. 346). I simply report what was told me.

Another way might be to drain the places where crawfishes are plentiful. But this hardly will be as efficient a means as desired. Drainage only lowers the level of the groundwater, and in the case of *C. carolinus*, which is the chief offender, we know that it digs down sometimes over three feet to reach the groundwater. In Rainier Park at Ohiopyle this species used to be very abundant, but the draining of the park has reduced its numbers. Still it is present there, and the chimneys are thrown up all over the lawn, where the holes must in places go down at least three feet before reaching water. Thus, although a decrease in numbers may be brought about by drainage, a complete extermination by this method must not be expected.

Another form of damage done by chimney-builders is known. They are reported to burrow into and to do damage to the dams on ponds, reservoirs, and rivers. (The levees of the Mississippi. See Ortmann, 1900, p. 1262.) No instances of this kind are known to me in Pennsylvania. In one case, at the reservoir of McGee Run, at Derry, Westmoreland County, I saw holes of *C. diogenes* not only along the banks, but also in the dam. The specimens were all young, and the holes small, since this reservoir has existed only for a few years. But it would not be astonishing if the crawfishes should gradually work deeper into the dam, finally causing serious damage.

VII. BEARING OF THE ABOVE STUDIES ON THE THEORY OF EVOLUTION.

Our observations on the Pennsylvania crawfishes, morphological, ecological, and geographical, serve to illustrate certain phases of the process of evolution, and certain theories propounded in connection with them. Naturally they do not elucidate this process in its fullest scope. Thus I shall only pick out a few points upon which my observations may have some bearing.

1. *The Mutation Theory of De Vries.*

The latest fashion in evolution theories is the so-called "mutation theory" of De Vries (De Vries, 1905). It is much discussed at present, and the general trend of opinion is that, although De Vries' idea of the origin of species may not hold good in all cases, he certainly has demonstrated at least one way by which species may be formed. It is generally maintained with emphasis that his experiments are beyond doubt and that the facts demonstrated by him cannot be denied.

This indeed is the case, and it would be lamentable if any of the statements presented by De Vries as facts should prove to be unreliable. I am decidedly of the opinion that the statements are correct, but I also hold that De Vries was not the first to bring the facts forward. They belong to a class that was known long ago. But furthermore, I believe that the conclusions drawn by De Vries from these facts are entirely wrong.

I recently have devoted several articles to demonstrate this, and shall not again go into detail here (see *Science*, May 11, August 17, and November 30, 1906).

However, I shall discuss here a special part of De Vries' theory, which concerns the distinction he makes between "fluctuating variation" and "mutation." The latter is said to be characterized by "sudden leaps," while the former is said to be by "small steps." Although De Vries sometimes does not lay much stress upon this distinction (see Copeland, 1904, p. 421), this difference is often regarded as paramount in his theory (see MacDougal, in *Popular Science Monthly*, vol. 39, 1906, p. 207). And since De Vries believes that species are formed only by mutation, it should be expected that the morphological differences between existing species should at least frequently exhibit signs of "sudden leaps." If such leaps are observed in our species of *Cambarus*, this would tend to support this part of De Vries' theory; if not, the theory that mutations are always or generally marked by discontinuity of variation, should be dropped.

2. *Species, Varieties, and Variations among the Pennsylvania Crawfishes.*

I have distinguished in the systematic part of this monograph seven species and one variety among the Pennsylvania crawfishes. Besides I have discussed another extralimital variety. This means that the characters distinguishing these forms are different in their taxonomic value, and the reasons for thus estimating them should be given.

The seven species of Pennsylvania belong to two subgenera, *Faxonius* and *Bartonius*, which are distinguished by very sharp differences in the male copulatory organs.

The subgenus *Faxonius* is represented in our state by three species: *C. limosus*, *C. propinquus*, and *C. obscurus*. The first is geographically, as well as morphologically, separated from the other two; and here again it is the shape of the male organs which serves as the chief distinguishing feature. Besides there are other characters, such as the shape and the spinosity of the carapace, which make it possible to recognize *C. limosus* at a glance. No transitional forms being present, the standing of *C. limosus* as a "good species" is beyond doubt.

It is different with *C. propinquus* and *obscurus*, and the extralimital form *C. sanborni*. These three resemble each other very closely, and it is hard, indeed impossible, without close examination to distinguish them. They also live under similar ecological conditions, and their ranges together form a unit, so that it is evident that they are closely allied genetically. The differences of *C. obscurus* from the other two forms are furnished by the "shoulder" of the male organ and the tubercles of the annulus of the female, together with the complete lack of the median keel of the rostrum. Other differences, such as sculpture and spinosity of the chelipeds, are of secondary value and not entirely reliable. But it must be emphasized that within the established range of *C. obscurus*, from Fish Creek in the southern part of the Panhandle of West Virginia to the upper Alleghany and the Genessee Rivers in McKean and Potter counties, and from Cheat River at the West Virginia state-line, to the upper Shenango River in Crawford County this species is remarkably uniform in the characters mentioned. No specimens have been found within this area which show the slightest tendency toward *C. propinquus*.

Thus, with reference to this form, the postulate that a species should be sharply and constantly separated from the coexisting allied forms is fulfilled (see Ortmann, 1896, p. 191) and accordingly I regard *C. obscurus* as a good species.

As regards *C. sanborni*, matters seem to be slightly different. It agrees in the shape of the sexual organs with *C. propinquus*, and differs only from the latter in the lack of a rostral keel and some minor features in the armature of the chelipeds. In the lack of a rostral keel it approaches *C. obscurus*, but always may be distinguished by the shape of the sexual organs. Its relation to *C. propinquus* remains doubtful. My observations do not cover the region in which possible transitions might be expected (northern and western Ohio), and thus I must leave this question open, and I follow Faxon in regarding *C. sanborni* as a variety of *C. propinquus*. But it should be possible to settle this question by proper investigation, and I would not be astonished if it should be finally discovered that *C. sanborni* actually is a good species, sharply and constantly separated from *C. propinquus*.

The subgenus *Bartonius* contains four species in Pennsylvania. One of them, *C. bartoni,* differs from the rest ecologically as well as morphologically. It is distinguished by a number of characters, and there is no possibility of morphologically intermediate forms, so that *C. bartoni* not only is a good species, but also belongs to a different section of the subgenus.

C. bartoni possesses in Pennsylvania a variety, *C. bartoni robustus,* which, according to my experience, is constant, and never runs into the typical form. It also seems to occupy a slightly different territory, although often found associated with the latter. These facts would justify us in regarding it as a good species. I have not done so in the systematic part, since the facts at hand are too meagre to finally decide this question. The range of *C. robustus* in Pennsylvania is only a small part of the area occupied by this form, and in the states of Ohio, New York, and in Canada, the conditions are entirely unknown. Furthermore a form similar to our *robustus,* although, as it seems to me, not entirely agreeing with it, has been reported from Virginia, Maryland, and Kentucky, and before particulars about the relation of this form to *C. bartoni* and to our *robustus* are known, we cannot judge as to the taxonomic position of *C. robustus.* Therefore I have refrained from modifying the position hitherto assumed, that this form is a variety of *C. bartoni.*

The other species of the subgenus *Bartonius* in Pennsylvania are *C. carolinus, C. monongalensis,* and *C. diogenes.* They belong to the *diogenes*-section, and all three are closely allied. *C. carolinus* and *monongalensis* are more nearly related to one another than to *C. diogenes.* The latter apparently is a more advanced form.

C. carolinus and *C. monongalensis* are distinguished by rather insignificant morphological characters, discovered in the shape of the rostrum and the armature of the chelipeds. But the difference in color is so striking that it is impossible to confound them in the field. Other characters also, although slight, hold good according to my experience, and I never have seen intermediate specimens. Moreover the distribution of these two forms is very characteristic, they being sharply separated topographically, and never being found associated at the same locality. Thus all requirements leading us to pronounce them good species are met. Of course this applies only to conditions in Pennsylvania, Maryland, and northern West Virginia; whether they are the same or different farther south remains to be seen.

C. diogenes is more sharply separated from the species just discussed, and there is no possibility of mistaking this species, more particularly as the color is markedly different. But the morphological characters are also very nicely expressed, so that in a case of a red (albinistic) specimen of this species I was not a moment in doubt that I had to deal with *C. diogenes,* and not with *C. carolinus,* although the latter was found associated with this form at this particular locality (Dunbar). There is no doubt that *C. diogenes* is a good species, and even when discovered in company with *C. monongalensis* or *C. carolinus* we found no intermediate forms which might render the identification uncertain.

As has been demonstrated above, there are two races of *C. diogenes* in Pennsylvania, an eastern and a western. They never have been distinguished before, and indeed are very similar, so that it is hard to tell them apart. But I think I am able to do so. The differences are very slight, but I never observed intermediate forms, and their existence is improbable, the ranges of the two races being widely distant from each other. The constancy of the differential characters being the only criterion of specific difference, while the amount of difference is of no consequence at all,[83] we might regard the eastern form as a different species from the western. This may prove to be the correct view, and then the eastern form should be called *C. diogenes* Girard, and the western possibly *C. obesus* Hagen. I have not taken this course in the systematic part, since our knowledge of *C. diogenes* is by no means complete. I know only the conditions in this state, but the eastern range of this species extends over large parts of the coastal plain, while the western occupies a vast territory reaching to the Rocky Mountains and the Gulf. It is also not impossible (although improbable) that the eastern and western areas are connected somewhere, (in Virginia?). Before this question is finally settled, and before we know more about the conditions under which *C. diogenes* occurs in the extralimital parts, it is best to refrain from expressing a positive opinion. Nevertheless it is quite possible that there is a tendency in *C. diogenes* to split into varieties and species. A variety has been distinguished in Louisiana.

We see that in certain forms my studies have led to a positive decision as to their taxonomic position. In other cases my observations must be completed and supplemented by additional evidence to be gathered in other parts of this country before a final opinion can be reached. The fault is not with the material at hand, but with the insufficiency of our knowledge of the extralimital parts.

As to *variations*, that is to say, occasional aberrations from the typical form, we have seen that such are extremely rare among the Pennsylvania crawfishes, and have in most cases the character of freaks. Some of them, however, are interesting from certain points of view.

No variations were discovered among one hundred and nineteen individuals of *C. limosus*. With reference to *C. propinquus* in Erie and Crawford Counties, I have pointed out that there is a certain amount of variation in the development of the keel of the rostrum, and in that of the spines and the carpopodite and meropodite of the chelipeds, and we have also seen that there is sometimes a notch on the anterior margin of the male organ. All these characters mark a certain inclination toward *C. obscurus* which will be discussed below.

---

[83] De Vries (1905, p. 127) talks of "an old rule in systematic botany, that no form is to be constituted a species upon the basis of a single character." This rule is entirely unknown to me in botany as well as in zoölogy.

The six hundred and eighty-seven specimens of *C. obscurus* at hand are, as has been seen above, very uniform in their characters. A tendency has been observed toward an increase of the spines of the meropodite of the cheliped in a direction from the northeast toward the southwest within the range of this species. Here we have apparently the first step toward the formation of a variety: a variation becomes more frequent in the southwestern part of the range, possibly in consequence of hereditary transmission, and begins to "breed true." But it is only the beginning of it, the varying form not being found to the exclusion of the original, and thus it remains " variation " only.

Other variations (mentioned p. 375 and 376) are very likely due to injuries received during life[84], and again others are of the character of freaks, namely the two cases of apparent hermaphroditism. One of these is rather interesting (Pl. XXXIX, Fig. 7^d and 7^e). Here the male sexual organs do not at all correspond to the typical form of this species, but approach in shape to that known in the *limosus*-section. It seems to me that we have to deal here with a case of atavism. The *limosus*-section has been regarded as the most primitive type of the subgenus *Faxonius*, on account of the very slightly separated tips of the copulatory organs. The *propinquus*-section is next to it, but here the tips are separated for a greater distance. It is quite probable that the latter section descended directly from the former, and it seems that in the instance discussed the sexual organs have reverted to the original *limosus*-type, and thus the assumption that the *propinquus*-section is a descendant of the *limosus*-section gains additional strength.

In the seven hundred and twenty-five specimens of *C. bartoni* we again have to emphasize the great uniformity of the characters. The variations discussed are rather insignificant, and consist chiefly in the shape of the rostrum and the size. A single individual has been observed in which one lateral spine of the carapace was present, apparently an atavistic feature. Other variations are of the hermaphroditic type.

No remarkable variations have been found in *C. carolinus*, and a few insignificant ones in *C. monongalensis.* The same is true of *C. diogenes*, leaving out of account the differences between the eastern and western forms. The most important variation is that of the width of the areola. In this there is a tendency toward regional restriction, but it is not complete. The wide areola, being a more primitive character, does not represent the variation, but the original condition, which is retained only in a small part of the range and is even there not general. It is a character that has a tendency to disappear and may be classed under atavism. A case of *albinism* has been observed in *C. diogenes.*

---

[84] Variations due to injuries are most frequently observed in the case of regeneration of the chelipeds. I did not mention them in the systematic part, since they are very common. If the claws are lost they are replaced by new claws, which differ from the old ones not only in size, but also in shape. The fingers are proportionally longer, and the palm proportionally shorter than in normal claws. This difference in shape remains even if the claws, after repeated moults, again attain a good size. Regenerated claws may always be recognized by the short palm and long fingers.

The conclusions from the above observations are that in the *Cambarus* forms of Pennsylvania the morphological characters are very constant, and that the variations observed are generally only slight, diverging very little from the typical conditions. Anything that looks like a "mutation" in De Vries' sense is entirely unknown, for the cases of hermaphroditism cannot be regarded as such, and the cases of atavism and albinism do not fall under it, being clearly of a "retrograde" character (De Vries, 1905, p. 121 *et seq.*).

Further, even between most of our well established species differences are so slight that they cannot be regarded as representing "mutations," that is to say, sudden leaps in a progressive direction (De Vries, *l. c.*, p. 141). This is most evident in the *propinquus*-section, where the three forms, two of which at least must be regarded as species, are distinguished by such insignificant characters that it is impossible to talk of "leaps" or of "sudden changes." The same is true of the differences of *C. carolinus*, *C. monongalensis*, and *C. diogenes*, the amount of the differences, although well marked, being very small, and the "gaps" between these species being infinitesimal. The only striking difference is in color, but before we know what causes the appearance of various colors we cannot express any judgment on this point.

Even in those species which are more isolated from the rest, the differences do not amount to much. In *C. bartoni* the depression of the carapace and the width of the areola differ only in the degree of the development from the same characters in the burrowing species. *C. limosus* is the most strongly marked species, but should not be compared with the other river-species of Pennsylvania, but with its nearest relations in southern Indiana (*C. indianensis* Hay), but then again the difference is small and consists only of quantitative changes in the same features.

Thus the assumption of De Vries, that species have originated by sudden leaps, does not find any support whatever in the conditions seen among the crawfishes of Pennsylvania. On the contrary the close affinity of most of them, and the comparative insignificance of the specific characters, supports the view that these species have originated out of rather slight variations from the original forms. If this is evident in so small a territory, further investigations only can emphasize this, for additional material can only bring these forms closer together. (See Merriam, 1906, p. 257.)

3. *Formation of Species by Isolation, as Exemplified by the Pennsylvania Crawfishes*

I have repeatedly maintained that the whole process of evolution in nature which ends in the formation of "species," and which, consequently, may be called "origin of species," is not subject to one single factor alone, such as "natural selection" or "isolation" or "mutation" but that it is absolutely necessary that several factors work together. (See Ortmann, 1896, p. 188 *et seq.*) Indeed none of these factors is new, and they have been discussed by various writers, but generally too much value has been attributed to one or the other of them to the detriment of the rest. I have insisted, on the contrary, that four factors are equally necessary to form species, namely: 1, variation; 2, inheritance; 3, natural selection; 4, separation (*l. c.*, p. 190).

Of these the last one, *Separation* or *Isolation*, is the one which forms species. To this is due the fact that the whole mass of organic beings to-day is divided up into a large number of units, which we call "species." If it had never existed or acted the process of evolution would have gone on nevertheless, but the organic world would not consist of *species;* but since separation always has acted, species are present. This does not imply that species should be everywhere well-marked. This process is going on all the time, and in many cases it is not yet finished, and thus it may be difficult sometimes to say whether a particular form is to be regarded as a species or not; but, as a rule, our inability to declare positively that a certain form is a species is only due to the insufficiency of our knowledge.

Separation (or isolation) should not only be conceived of in its broad topographical and climatic aspect, but is, as I have always maintained, largely also ecological. (See "bionomic separation," *l. c.*, p. 190.)[85] That it may occur under several forms is amply demonstrated by the Pennsylvania crawfishes, and some form or other of isolation is evident in every case *without exception.* Both topographical and ecological separation are recognizable in our material, while climatic separation is not observed on account of the insignificant differences of climate in the region investigated.

---

[85] "Barriers" are not necessary. Merriam, 1906, p. 248, thinks that the existence of sharp barriers is necessary for isolation; where such are absent he prefers to use the term "divarication." Possibly the term "habitudinal segregation," introduced by Gulick, 1905, p. 49, and 53 *et seq.* would be appropriate.

(*a*) *C. limosus.*

It has been repeatedly emphasized above, as well as in a previous paper, that this species is well isolated morphologically and geographically. I have introduced it as one of the examples for the rule that "morphologically isolated species occupy isolated stations" (Ortman, 1905*b*, p. 127), and also for the rule that "discontinuity of distribution is a proof of antiquity" (*ibid.*). Both rules are beautifully illustrated by this species, particularly in contrast to the other rule that "closely allied-species occupy neighboring areas." Thus not only the effect of isolation, as producing species, is evident in *C. limosus*, but it is also seen that the degree of isolation is in direct proportion to the sharpness of the expression of the specific characters. *C. limosus* is geographically the most sharply isolated species of our crawfishes, its area being several hundred miles distant from that of the most closely allied forms in Indiana and Kentucky. Correspondingly it is also morphologically well marked, being sharply distinguished from the other Pennsylvanian species, as well as from species in the west which are closely related to it. Isolation in this case is purely topographical, since the ecological habits of *C. indianensis* seem to be similar, (Hay, 1896, p. 495); though another allied form, *C. sloani*, differs slightly ecologically, (Faxon, 1885, p. 90).

(*b*) *C. propinquus, C. propinquus sanborni, C. obscurus.*

These three forms, as far as our present knowledge goes, are sharply separated topographically, while they agree with each other ecologically, but the topographical boundaries between them are not everywhere uniformly sharp. In fact, the ranges of these three forms are connected on the one side by the Ohio River, on the other side by the basin of the Great Lakes.

As we have seen above, the present connection of these forms is a secondary feature developed during the latter part of the Glacial Period, while anterior to this, at the beginning of the Glacial epoch, different conditions prevailed, which were different in turn from those of still earlier times. The history of these forms was probably as follows. At the end of the Tertiary a form corresponding to these three crawfishes existed in the drainage of the Erigan River. Probably there was only a single species resembling the present *C. propinquus*. This species lived in the Erigan River, as well as in its southern tributaries, and there was no chance for it to split up into different species, although variations may have occurred. When the advancing ice of the Glacial Period covered the Erigan River and thus separated the southern tributaries from each other, the latter formed lakes, and later, by overflow (or other means) they were connected again. Thus the present Ohio was created. The temporary isolation of these rivers at the beginning of the Glacial epoch had its effect upon the crawfishes living in them. They developed into as many species as there were rivers (three). Probably there was already in Tertiary times a tendency within the Erigan drainage to form variations and even geographical varieties, but the fact that these forms (at least two of them) assumed the character of species is due to the physiographical features of the *earlier Glacial Period.*

After the Ohio was formed, and the connection between the areas of these species was reestablished, there must have been a tendency among them to mix along the course of the Ohio River. How it was in the case of *C. propinquus* and *C. sanborni* we do not know. But I have investigated the facts in the case of *C. sanborni* and *C. obscurus.* Where they come together in the neighborhood of New Martinsville, West Virginia, *C. sanborni* shows no tendency at all to go up the river, no trace of it being found above New Martinsville. This apparently is due to the greater difficulty of ascending the river and to contend with a species which is firmly established there. On the other hand *C. obscurus* apparently has gone down the river, and has invaded the original territory of *C. sanborni,* but it has done so only to a small extent. For, although it is easier to descend a river, the fact that the region invaded is occupied by another species with the same ecological habits must make it rather difficult to oust the latter. Thus, although *C. obscurus* has the advantage over *C. sanborni,* being favored in its migration by the fact that it is here downstream, this advantage is only a slight one, and did not enable *C. obscurus* to occupy any of the territory of *C. sanborni* to the exclusion of the latter. It is found here associated with it, but its numbers are small, and the original form still prevails.

A curious fact, however, has been observed. I have pointed out (p. 367 and p. 434) that the specimens of *C. sanborni* captured in Fishing Creek at New Martinsville showed in certain characters an inclination toward *C. obscurus.* This suggests hybridization. Of course it is impossible to ascertain this positively without experiments, but it seems that a crossing between these two forms is not altogether impossible, for the shape of the sexual organs is very similar in both. They are generally very closely allied, and further, their breeding seasons are identical, so that kyesamechania[86] probably does not exist. This is further suggested by the conditions observed in the Lake Erie drainage in Pennsylvania. Here *C. propinquus* and *C. obscurus* come together, and again we pointed out (p. 365) that *C. propinquus* in this region has a tendency towards *C. obscurus.* In both cases hybridization would easily explain matters.

---

[86] Impossibility of crossing, due to any cause, mechanical, physiological, or ecological, see Eimer, 1895, p. 14. Gulick (1905, p. 95) calls this "Impregnational Isolation." Under this head falls also Romanes' "physiological isolation."

Even if it should be the case that *C. obscurus* may cross with *C. propinquus* and *C. propinquus sanborni*, this does not invalidate its standing as a species, for we have numerous examples in nature in which true species form hybrids.

Thus we see that these three species, the origin of which as species belongs to the beginning of the Glacial time, have come together again; but each seems to remain in its original area, and where they come into actual contact the one species is hardly able to oust the other. To a small degree hybridization seems to be possible at the points of contact. The assumption that *C. sanborni* might be a hybrid between *C. propinquus* and *C. obscurus* is rendered impossible by the exclusive presence of *C. sanborni* all over its range (excepting Fishing Creek), without any trace of the two other species.

It remains to consider the question what the relation of the specific characters to isolation may be. We see that in the case of *C. obscurus* it is chiefly the "shoulder" of the male sexual organ which distinguishes this species. This shoulder is found at a place where an external stimulus acts upon this organ, namely, just where it is touched by the fifth pereiopod in the act of copulation. A similar shoulder is found in many other species of *Cambarus* of different groups and even subgenera, and thus it is highly probable that it is this external stimulus which induces the development of this feature. But this does not afford us an explanation why this shoulder did not develop in other species, especially in *C. propinquus.* At present I am unable to answer this question. The fact remains that we have to deal with a specific character, which is clearly due to an external stimulus,[87] and I have always held the opinion that every variation is invariably caused by a reaction of the organism to some external influence. (See Ortmann, 1896, p. 188, and 1898, p. 157.) But the view that acquired characters are transmissible is not fashionable, although now admitted by its chief adversary, Weismann. In consequence of the modern tendency to deny the effect of external causes upon variation, at any rate to deny the possibility of the hereditary transmission of such variations, not much attention has been paid to the mutual relations between external stimuli and the reaction of the organism upon them. But here I think much room for investigation is left. In the present case the reaction of the organism upon the external stimulus caused by the contact of the fifth pereiopod with the sexual organ is to form at the point of contact a notch or angle (shoulder) on the sexual organ.

This reaction may be slightly advantageous, but it is not absolutely necessary, for we see that there are many other species in which this reaction has not taken place, even among the most closely allied forms, which are nevertheless well off and flourishing. In other words, the "selectional value" of this character is practically at the zero-mark. This demonstrates again that the conception of "natural selection" as "selection of the fittest" is incorrect. With regard to fitness there are many characters which are entirely indifferent, and this is one of them. The absence or presence of a rostral keel, and of tubercles in the case of the female annulus, the other specific differences of these forms, belong to the same class. We thus see that natural selection has played no part in the development of these characters of these species. But this does not imply that selection has had nothing to do with the evolution of these species, on the contrary this factor has always acted, and if these characters had not been fit to survive, the species would not have been able to survive. Natural selection (in the modified sense, according to Pfeffer, see Ortmann, 1896, p. 176), resulted in the fact that the *propinquus*-group, such as it actually is, is able to live and to flourish, but it is not responsible for the splitting up of this group into two or three species.

---

[87] Under "pressure of the environment," as Merriam puts it (1906, p. 244).

The latter fact is entirely due to *isolation*. In the present case the isolation was in effect only during a short period in the past, but it was enough to differentiate several species. At the present time there is a tendency to undo this effect. These species are beginning to mingle again. But this process has not yet progressed far, and for several reasons will very likely be slow in future. It is hard to say what the outcome will be, whether we shall have a hybrid form, or whether one will suppress the others. *C. obscurus* is the most advanced form, and also seems to be slightly more vigorous than the others. Thus it may finally overrun them and crowd them out, unless it is in turn conquered by a still more vigorous from, *C. rusticus*, advancing from the southwest.

From the above discussion we see that whatever may have been the processes of variation and of natural selection, or independently of what we may think of the possibility of the inheritance of acquired characters, the fact that the *propinquus*-group has split up into species is solely due to isolation, which in this case is strictly topographical. We have here three forms with identical ecological habits, in which topographical isolation is evident, illustrating the rule that "closely allied species occupy neighboring areas." (See Ortmann, 1905*b*, p. 127, Jordan, Science, Nov. 3, 1905, p. 546, and Merriam, 1906, p. 248, *et seq.*)

(*c*) *C. bartoni.*

This species is morphologically well isolated from the other Pennsylvanian species, and also has peculiar ecological habits. Being found all over the state it necessarily comes into contact with all the other species and is often found associated with them. This is preëminently the case with the river forms, *C. limosus, C. obscurus,* and *C. propinquus.*

Here we have an instance in which at a given locality two species may be found side by side. This, however, is due to secondary processes. Originally each of the two species had a different center of radiation, and thus we again see the action of isolation. The center of *C. bartoni* lies in the mountains of the Appalachian system; the common center of *C. limosus* and the *propinquus*-group is in the central basin of the Mississippi, and the special center of *C. limosus* in the coastal plain, and that of the *propinquus*-group in the Erigan and Lower Ohio drainage.

Nevertheless these species came together (see Ortmann, 1896, p. 186), but the migration was in different directions, the river species coming up the rivers, while *C. bartoni* migrated down stream. Although living side by side there is no danger of hybridisation, since their morphological differences are such that kyesamechania exists. The different shape of the sexual organs of *C. bartoni* from that in the subgenus *Faxonius* precludes any idea of their being able to cross. Such cases do not offer anything remarkable, since the occupation of and the association at the same locality of different forms coming from different directions, and not being closely allied, is the general rule in any ecological community (*biocenosis*).

Conditions are slightly different in the cases where *C. bartoni* is found in close proximity to the chimney-builders. Here there is closer affinity, but also it seems here that these species are so far separated morphologically that kyesamechania exists, although the shape of the copulatory organs is similar. Moreover, wherever *C. bartoni* comes into contact with the burrowing species it generally occupies situations slightly different from those preferred by the chimney-builders. It favors running water in open streams, while the burrowers are found in holes at a certain distance from the streams. Nevertheless, *C. bartoni* is sometimes found in burrows and in springs close to the one or the other of the burrowers (it is even found in the holes of the latter, see p. 414), but in such cases we have again the same conditions as above: different species coming from different centers occupy the same locality.

Yet as a rule *C. bartoni* occupies a different habitat from the burrowers, even if found close to the latter. A fine illustration of this is in Nine-Mile Run, near Pittsburgh. Here three species, *C. bartoni, C. monongalensis,* and *C. diogenes,* are found together upon a space hardly more than twenty feet square. The locality is a pile of talus swept down into the valley of Nine-Mile Run by a small stream. The stream comes through an insignificant ravine, and spreads out over the talus, forming a kind of a delta, rendering the lower parts of the pile of talus rather swampy. At the upper end of the talus, in the outcrop of sandstone rock, and not far (about fifteen feet) from the bed of the spring, is a copious spring, the water of which runs directly into the clay and humus of the pile of talus, in a large part underground. *C. bartoni* is found in the small stream under stones; *C. monongalensis* is found at and immediately below the spring referred to; and *C. diogenes* is abundant all over the pile of talus down to the bottom of the valley. At the upper end of the pile of talus is the place where all three species come close together, but each is subject to different ecological conditions.

Similar conditions have been frequently observed, and we thus have here the occupation of the same localities by closely allied species, which differ ecologically, that is to say, *topographical* isolation is not observed here, but the isolation is *ecological*, and the differentiation of the chimney-builders from *C. bartoni* very likely is connected with and largely due to the latter.

(*d*) *C. carolinus and C. monongalensis.*

We have seen that these two species are very closely allied, but that the distinguishing characters are constant. Ecologically they are similar, so that hybridisation might occur when they come together. The latter case, however, has never been observed, at least in Pennsylvania, Maryland, and northern West Virginia. The western escarpment of the Chestnut Ridge forms a sharp boundary between them. This case corresponds to that observed in the western river-species (*propinquus*-group). Two species identical in their ecological habits are separated topographically. But in this case the barrier separating them is of a different character. What the essential feature of this barrier is, is hard to say. Chestnut Ridge in many respects forms a boundary. Altitude seems to play a part, but whether it is paramount is doubtful. Absence of extensive deposits of clay on the western side of this ridge on account of the destruction of the Old Tertiary base-level by subsequent erosion, may also be of importance. Further studies in West Virginia surely will lead to a solution of the question, but this much is certain, that these two species again illustrate the rule that "closely allied species occupy neighboring areas," and further they illustrate the fact that specific differentiation is due to isolation, which is topographical in this case.

What are the actual causes of the difference of the specific characters (color, shape of rostrum, and sculpture of chelipeds), that is to say, what external influences are responsible for them is even more obscure, as it is in the case of the *propinquus*-group.

(*e*) *C. diogenes.*

C. diogenes is sharply separated from the other chimney-builders, but resembles them ecologically to a certain degree. In Pennsylvania it comes into contact with them, but in the case of *C. carolinus* this has been observed only once, while it is more frequent in the case of *C. monongalensis.* However, intermediate forms have never been observed, so that we must assume that kyesamechania prevents crossing.

In both cases, with reference to *C. carolinus* as well as *C. monongalensis*, it is to be remarked that whenever one of these is found associated with *C. diogenes* it is always only a contact, not a real mixing of both forms. This is best observed in the case of *C. monongalensis* and *C. diogenes.* All over the range of *C. monongalensis* in southwestern Pennsylvania *C. diogenes* is also found. But as has been stated (p. 417 and 458), although they frequently dwell at the same localities they do not occupy the identical locations, *C. diogenes* belonging to a lower level than *C. monongalensis.* Thus we see again a separation, which is primarily expressed in the difference of altitude. Whether the latter is most important seems doubtful. It has been stated that *C. monongalensis* prefers spring-water, while *C. diogenes* lives mostly in swamps, where the water is more or less stagnant and not so cool in summer. (Compare the instance from Nine-Mile Run given above.) But, whatever may be the essential feature which separates both species, it is clear that it is an ecological factor, and, when these two species are found together, it is at a place where the ecological conditions favorable to them come together.

That *C. diogenes* depends on different ecological laws from *C. monongalensis* is also evident from the fact that the former has, outside of Pennsylvania, an entirely different range.

Thus we have here a case similar to that of *C. bartoni* when it associates with the burrowing forms. Two allied species occupy (in Pennsylvania) almost the same territory, and are not separated topographically, but their ecological separation is evident, and very likely is connected with their specific differentiation.

In the two races *C. diogenes*, the eastern and western, we again see the influence of separation. According to our theory that the area of *C. diogenes* was a unit in Preglacial times, and that it was separated by the advancing ice into an eastern and a western section, which subsequently remained separate, we must expect, if isolation effects specific differentiation, that the eastern and western form of *C. diogenes* should show at least a tendency to develop differential characters of specific value. This is indeed the case, as we have seen above (p. 401 et seq).

Isolation, or Habitudinal Segregation, as the factor forming species, is thus clearly seen in every case discussed. We may condense the results obtained in the following sentences.

1. The normal case is when two closely allied species, possessing identical or nearly identical ecological habits occupy separated areas, which lie close together but do not overlap. (Examples: *propinquus*-group; *C. carolinus* and *C. monongalensis.*)

2. Whenever allied species are found in one and the same locality (overlapping), isolation becomes apparent in the following forms.

(*a*) The two species have different centers of origin, that is to say, they were separated formerly, but occupied the same territory subsequently. In this case, if very closely allied, hybridization may be possible (*C. obscurus* and *C. sanborni* at New Martinsville, and *C. obscurus* and *C. propinquus* in the Lake Erie drainage), if no kyesamechania exists. If the latter is present, which always means that the two species in question are less closely allied, the two species may actually live side by side under identical conditions (*C. bartoni* and the river-species), or one may conquer and suppress the other. No instances of the latter kind are known in Pennsylvania, but may possibly occur in southwestern Ohio and in Indiana, between *C. rusticus* and *C. propinquus.*

(*b*) If the centers of origin are more or less identical (absolute identity is hardly possible), the two species always differ ecologically, and although living at the same localities, prefer different surroundings. In this case they are not so closely associated, and they generally remain at a certain distance from one another, although their general areas are overlapping. Under such conditions hybridisation might occur, but it has not been observed in Pennsylvania, and the species existing under such conditions are probably separated by kyesamechania. (Example: *C. diogenes* and *monongalensis.*)

Case (*a*) and (*b*) may be combined, that is to say, two species living together may have different centers of origin and may be ecologically different. This is seen in the example of *C. bartoni* and the burrowing species.

I believe that in every case where closely allied species overlap in parts of their ranges a close investigation will reveal that one or the other of the above cases is realized. Isolation is, in my opinion, a necessary factor in the differentiation of species, and I do not think that a case ever will be discovered where two closely allied species possess precisely the same distribution. But in order to ascertain this a mere superficial knowledge of the species in question and their range is insufficient, and every case should be investigated as exactly as possible, in a manner similar to the above studies.

BIBLIOGRAPHY.

1902. Abbe, C. The Physiography of Garrett County. Maryland Geological Survey, Garrett County.

1873. Abbott, C. C. Notes on the Habits of Certain Crawfish. *American Naturalist*, VII, p. 80.

1884. Abbott, C. C. Are the "Chimneys" of Burrowing Crayfish Designed? *American Naturalist*, XVIII, p. 1,157.

1885. Abbott, C. C. How the Burrowing Crayfish Works. *The Inland Monthly*, I, p. 31.

1902. Adams, C. C. The Southern United States as a Center of Geographic Distribution of Flora and Fauna. *Biol. Bull.*, III, p. 115.

1905. Adams, C. C. The Postglacial Dispersal of the North American Biota. *Biol. Bull.*, IX, p. 53.

1895. Andrews, E. A. Conjugation in an American Crayfish. *American Naturalist*, XXIX, p. 867.

1904. Andrews, E. A. Breeding Habits of Crayfish. *American Naturalist*, XXXVIII, p. 165.

1859. Bell, H. On the Natural History of the Gulf of St. Lawrence, and the Distribution of the Mollusca of Eastern Canada. *Canadian Naturalist and Geologist*, IV, p. 210.

1877. Bundy, W. F. On the Cambari of Northern Indiana. *Proc. Acad. Nat. Sciences of Philadelphia*, p. 171.

1882. Bundy, W. F. A List of the Crustacea of Wisconsin, with Notes on Some New or Little Known Species. *Trans. Wisconsin Academy*, V, p. 177.

1883. Bundy, W. F. The Crustacean Fauna of Wisconsin, with Descriptions of Little Known Species of Cambarus. *Geol. Surv. Wisc.*, 1873–79, I, p. 402.

1903. Campbell, M. R. Geographic Development of Northern Pennsylvania and Southern New York. *Bull. Geol. Soc. Amer.*, XIV, p. 277.

1880. Carll, J. F. The Geology of the Oil Region. *Second Geol. Surv. Pa.*, I3.

1904. Copeland, E. B. The Variation of some California Plants. *Botan. Gazette*, XXXVIII, p. 401.

1889. Davis, W. M. The Rivers and Valleys of Pennsylvania. *National Geogr. Mag.*, I, p. 183.

1844. De Kay, J. E. Zoology of New York, Part 6, Crustacea, p. 22.

1905. De Vries, H. Species and Varieties, Their Origin by Mutation. Edited by D. T. MacDougal.

1895. Eimer, G. H. T. Die Artbildung und Verwandtschaft bei den Schmetterlingen. 2. Teil.

1846. Erichson, W. F. Uebersicht der Arten der Gattung Astacus. *Arch. f. Naturg Jahrg.*, XII, p. 86.

1798. Fabricius, J. C. Supplementum Entomologiæ Systematicæ.

1896. Fairchild, H. L. Glacial Genessee Lakes. *Bull. Geol. Soc. Amer.*, VII, p. 423.

1884*a*. Faxon, W. On the So-called Dimorphism in the Genus Cambarus. *Amer. Journ. Sci.*, XXVII, p. 42.

1884*b*. Faxon, W. Descriptions of New Species of Cambarus. *Proc. Amer. Acad. Science*, XX, p. 107.

1885*a*. Faxon, W. A Revision of the Astacidæ. *Mem. Mus. Harvard*, X.

1885*b*. Faxon, W. A List of the Astacidæ in the U. S. National Museum. *Pr. U. S. Nat. Mus.*, 1885, p. 356.

1885*c*. Faxon, W. Preliminary Catalogue of the Crayfishes of Kansas. *Bull. Washburn Laboratory*, Topeka, I, p. 140.

1890. Faxon, W. Notes on North American Crayfishes, Family Astacidæ. *Pr. U. S. Nat. Mus.*, XII, p. 619.

1898. Faxon, W. Observations on the Astacidæ in the U. S. National Museum and in the Museum of Comparative Zoology, with Descriptions of New Species. *Pr. U. S. Nat. Mus.*, XX, p. 643.

1876. Forbes, S. A. List of Illinois Crustacea, with Descriptions of New Species. *Bull. Illin. Mus.*, I, p. 3.

1890. Foshay, P. M. Preglacial Drainage and Recent Geological History of Western Pennsylvania. *Amer. Journ. Sci.*, XL, p. 397.

1887. Ganong, W. F. The Crayfish in New Brunswick. *Bull. Nat. Hist. Soc. N. Brunsw.*, VI, p. 74.

1850. Gibbes, L. R. On the Carcinological Collections of the United States. *Pr. Amer. Assoc.*, III, p. 167.

1852. Girard, C. A Revision of the North American Astaci, with Observations on their Habits and Geographical Distribution. *Pr. Acad. Nat. Sciences, Philadelphia*, VI, p. 87.

1833. Goodman, J. D. Rambles of a Naturalist.[88]

1841. Gould, A. A. Report on the Invertebrata of Massachusetts, p. 330.

1901. Grabau, A. W. Guide to the Geology and Paleontology of Niagara Falls and Vicinity. *Bull. N. Y. State Museum*, XLV.

1905. Gulick, J. T. Evolution, Racial and Habitudinal. *Carnegie Institution of Washington.*

1870. Hagen, H. A. Monograph of the North American Astacidæ. *Illustr. Catal. Mus. Harvard*, III.

---

[88] I have only seen a copy of a later edition, in "American Natural History," Vol. II, 3d ed., 1842, p. 293 (Library of Acad. Nat. Sc., Phila.). Girard and Hagen quote this work as of 1833; Faxon (1885*a*, p. 63) as of 1859.

1835. Harlan, R. Description of Three Species of the Genus Astacus inhabiting the United States. *Medic. and Physic. Research*, p. 229.

1900. Harris, J. A. Annotated Catalogue of the Crayfishes of Kansas. *Kans. Univ. Quart.*, IX, p. 263.

1903. Harris, J. A. The Habits of Cambarus. *Amer. Natural.*, XXXVII, p. 601.

1896. Hay, W. P. The Crawfishes of the State of Indiana. *20th Rep. Indiana Geol. Surv.*, p. 475.

1899. Hay, W. P. Synopsis of North American Invertebrates. 6. The Astacidæ of North America. *Americ. Natural.*, XXXIII, p. 957.

1902*a*. Hay, W. P. Observations on the Crustacean Fauna of the Region about Mammoth Cave, Kentucky. *Pr. U. S. Nat. Mus.*, XXV, p. 223.

1902*b*. Hay, W. P. On the Proper Application of the Name *Cambarus carolinus* Erichson. *Pr. Biol. Soc. Washington*, XV, p. 38.

1905. Hay, W. P. Instances of Hermaphroditism in Crayfishes. *Smithson. Misc. Coll.*, XLVIII, p. 222.

1903. Hice, R. R. Northward Flow of Ancient Beaver River. *Bull. Geol. Soc. Amer.*, XIV, p. 297.

1904. Hollister. See Leighton and Hollister.

1905. Hoyt, J. C. and Anderson R. H. Hydrography of the Susquehanna River Drainage Basin. *U. S. Geol. Surv., Water Suppl. and Irrig. Papers*, 109.

1904. Hulbert, A. B. The Great American Canals, Vol. II. (Historic Highways of America, Vol. XIII.)

1903. Jenkins, H. M. Pennsylvania, Colonial and Federal. Vol. III.

1903. Jillson, B. C. River Terraces in and near Pittsburgh. *Tr. Acad. Sci. and Art of Pittsburg.*

1900. Klein, T. B. The Canals of Pennsylvania, and the Systems of Internal Improvements of the Commonwealth. *Ann. Rep. Secret. Intern. Aff. of Pa.*, 28, Part 4, p. LXIV.

1903. Leighton, M. O. Normal and Polluted Waters in Northeastern United States. *U. S. Geol. Surv., Water Suppl. and Irrig. Papers*, 79.

1904. Leighton, M. C. and Hollister, G. B. Quality of Water in the Susquehanna Drainage Basin, with an Introductory Chapter on Physiographic Features. *U. S. Geol. Surv., Water Suppl. and Irrig. Papers*, 108.

1902. Leverett, F. Glacial Formations and Drainage Features of the Erie and Ohio Basins. *Monogr. U. S. Geol. Surv.*, XLI.

1884. Lewis, H. C. Report on the Terminal Moraine. *Second Geol. Surv. Pa.*, Z.

1888. McGee, W J Three Formations of the Middle Atlantic Slope. *Amer. Journ. Sci.*, XXXV, p. 120, 328, 367, 448.

1906. Merriam, C. H. Is Mutation a Factor in the Evolution of the Higher Vertebrates? *Science*, N. S., XXIII, Febr. 16, p. 241.

1837. Milne-Edward, H. Histoire Naturelle des Crustacés. II, p. 331.

1902. Newsom, J. F. Drainage of Southern Indiana. *Journ. Geol.*, X, p. 166.

1891. Ortmann, A. E. Die Decapoden Krebse des Strassburger Museums. III. *Zool. Jahrb., Syst.* VI, p. 12.

1896. Ortmann, A. E. On Natural Selection and Separation. *Pr. Amer. Philos. Soc.*, XXXV, p. 175.

1898. Ortmann, A. E. Ueber Keimvariation. *Biolog. Centralbl.*, XVIII, p. 139.

1899–1900. Ortmann, A. E. Bronn's Klassen und Ordnungen des Tierreichs, V, Crust. 2, p. 1210, 1242.

1905*a*. Ortmann, A. E. The Crawfishes of Western Pennsylvania. *Ann. Carnegie Mus.*, III, p. 387.

1905*b*. Ortmann, A. E. The Mutual Affinities of the Species of the Genus Cambarus and their Dispersal over the United States. *Pr. Amer. Philos. Soc.*, XLIV, p. 91.

1898. Osborn, R. C. and Williamson, E. B. The Crayfish of Ohio. *Sixth Ann. Rep. Ohio State Acad. Sci.*, p. 21.

1905. Paulmier, F. C. Higher Crustacea of New York City. *Bull. N. Y. State Mus.*, 91, p. 117.

1896. Powell, J. W. Physiographic Regions of the United States. (The Physiography of the United States. *Nat. Geogr. Mag.*, p. 65.)

1874. Putnam, F. W. Remarks on the Mammoth Cave and Some of Its Animals. *Bull. Essex Inst.*, VI, p. 191.

1817. Rafinesque, C. S. Synopsis of Four New Genera and Ten New Species of Crustacea Found in the United States. *Americ. Monthly Magazine*, II, p. 40.

1905. Rathbun, M. J. Fauna of New England. 5. List of the Crustacea. *Occas. Papers. Boston Soc. Nat. Hist.*, VII, p. 18.

1886. Ridgway, R. Nomenclature of Colors.

1617. Say, T. An Account of the Crustacea of the United States. *Journ. Acad. Nat. Sci. Philadelphia*, I, p. 167.

1896. Shufeldt, R. W. The Chimneys of Burrowing Crayfish. *The Observer*, VII, No. 3, p. 85.

1874. Smith, S. I. The Crustacea of the Freshwaters of the Northern United States, *Rep. U. S. Fish Comm. for 1872 and 1873*, p. 637.

1881. Spencer, J. W. Discovery of the Preglacial Outlet of the Basin of Lake Erie into that of Lake Ontario; with Notes on the Origin of our Lower Great Lakes. *Pr. Amer. Philos. Soc.*, XIX, p. 300.

1894. Spencer, J. W. A Review of the History of the Great Lakes. *Amer. Geologist*, XIV, p. 289.

1878. Stevenson, J. J. The Ligonier Valley. *Second Geol. Surv. Pa.*, K3.

1884. Tarr, R. S. Habits of Burrowing Crayfishes in the United States. *Nature,* XXX, p. 127.

1842. Thompson, Z. Natural History of Vermont, I, p. 170.

1903. Tight, W. G. Drainage Modifications in Southeastern Ohio and Adjacent Parts of West Virginia and Kentucky. *U. S. Geol. Surv., Profess. Papers* XIII.

1886. Underwood, L. M. List of the Described Species of Freshwater Crustacea from America North of Mexico. *Bull. Ill. State Laboratory,* II, p. 365.

1896. Ward, H. B. A Biological Examination of Lake Michigan in the Traverse Bay Region. *Bull. Mich. Fish. Comm.,* VI, p. 15.

1896. White, I. C. Origin of the High Terrace Deposits of the Monongahela River. *Amer. Geologist,* XVIII, p. 368.

1899. Williamson, E. B. Notes on Ohio Astacidæ. *Seventh Ann. Rep. Ohio State Acad.,* p. 47.

1901. Williamson, E. B. The Crayfish of Allegheny County, Pa. *Ann. Carn. Mus.,* I, p. 8.

1905. Williamson, E. B. Crayfishes from Kentucky. *Ohio Natural.,* V, p. 310.

1896. Willis, B. The Northern Appalachians. (The Physiography of the United States. *Nat. Geogr. Mag.,* p. 169.)

EXPLANATION OF PLATES.

Plate A.

Fig. 1. *Cambarus obscurus* Hagen. Male of the first form, natural size. Collected by the writer, Sept. 7, 1905, in the Alleghany River, Sandy Creek, Allegheny County.

Fig. 2. *Cambarus obscurus* Hagen. Female, natural size. From same locality.

Fig. 3. *Cambarus diogenes* Girard. Male of the first form, natural size. Collected by the writer, Aug. 26, 1905, at Baden, Beaver County.

Fig. 4. *Cambarus carolinus* Erichson. Female, natural size. Collected by the writer, Sept. 5, 1905, at Rainier Park, Ohiopyle, Fayette County.

Plate B.

Fig. 1. *Cambarus bartoni* (Fabricius). Male of first form, natural size. Collected by the writer, Aug. 7, 1905, in Fern Hollow, Pittsburgh.

Fig. 2. *Cambarus bartoni robustus* (Girard). Female, natural size. Collected by Miss G. Kinzer, Aug. 27, 1905, at Sixteen Mile Creek, Northeast, Erie County.

Fig. 3. *Cambarus limosus* (Rafinesque). Female, natural size. Collected by the writer, Sept. 10, 1905, in the Schuylkill Canal, Manayunk, Philadelphia County.

Fig. 4. *Cambarus monongalensis* Ortmann. Female, natural size. Collected by the writer, Aug. 18, 1905, at Edgewood Park, Allegheny County.

Plate XXXIX.

Fig. 1. *Cambarus bartoni* (Fabricius). Rostrum. All figures $\frac{4}{1}$.

1*a*. Female, 70 mm. long. Collected by the writer, June 3, 1904, in North Versailles Township, Allegheny County, opposite Stewart. Catalogue number 74.327. Shape very broad, margins parallel. Not rare in western Pennsylvania.

1*b*. Female, 52 mm. long. Collected by the writer, Aug. 22, 1905, at Squaw Run, Allegheny County. Catalogue number 74.626. Shape typical; very frequent.

1*c*. Male, first form, 63 mm. long. Collected by the writer, Sept. 16, 1904, at Valley Forge, Chester County. Catalogue number 74.413. Shape typical, and characteristic of eastern specimens, but also found in the west.

1*d*. Young male, second form, 34 mm. long. Collected by the writer, Aug. 22, 1905, in Squaw Run, Allegheny County. Catalogue number 74.626. Usual shape in young specimens.

1*e*. Young female, 21 mm. long. Collected by the writer, June 25, 1904, in Jacob's Creek, Laurelville, Fayette County. Catalogue number 74.356. Slightly longer than usual, but not rare in young specimens.

1*f*. Male, first form, 78 mm. long. Collected by the writer, May 27, 1904, in Squaw Run, Allegheny County. Catalogue number 74.320. Unusually short and strongly tapering, with exceptionally thick margin.

FIG. 2. *Cambarus bartoni robustus* (Girard). Rostrum. $\frac{4}{1}$.

2*a*. Female, 89 mm. long. Collected by the writer Oct. 4, 1904, in Temple Creek, Albion, Erie County. Catalogue number 74.435. Normal shape.

2*b*. Young female, 18 mm. long. Collected by Miss G. Kinzer, Aug. 27, 1905, in Sixteen-Mile Creek, Northeast, Erie County. Catalogue number 74.630. Normal shape in young specimens.

FIG. 3. *Cambarus carolinus* Erichson, Rostrum. $\frac{4}{1}$.

3*a*. Male, first form, 66 mm. long. Collected by the writer, Sept. 5, 1905, at Ohiopyle, Fayette County. Catalogue number 74.640. Normal shape.

3*b*. Male, second form, 30 mm. long. Collected by the writer, June 11, 1904, at Indian Creek, Fayette County. Catalogue number 74.365. Shape exceptional. Most extreme case as regards convergence of margins.

FIG. 4. *Cambarus monongalensis* Ortman. Rostrum. $\frac{4}{1}$.

4*a*. Male, first form, 63.5 mm. long. (Type.) Collected by the writer, May 21, 1905, a Edgewood Park, Allegheny County. Catalogue number 74.316. Normal shape.

4*b*. Female, 73 mm. long. Collected by the writer, Oct. 12, 1904, at Hill, Westmoreland County. Catalogue number, 74.449. Shape unusually broad, and margins almost parallel. Most extreme case in this direction, standing rather isolated.

FIG. 5. *Cambarus limosus* (Rafinesque). Left first pleopod of male, first form. $\frac{3}{1}$.

5*a*. Inner view. Collected by the writer, Sept. 19, 1904, in Marcus Hook Creek, Marcus Hook, Delaware County. Catalogue number 74.423.

5*b*. Posterior view of same.

FIG. 6. *Cambarus propinquus* Girard. Left first pleopod of male. $\frac{3}{1}$.

6. Inner view, male, first form. Collected by the writer, Oct. 4, 1904, in Temple Creek, Albion, Erie County. Catalogue number 74.439.

6*b*. Inner view, male, second form. Collected by the writer, June 7, 1904, in a tributary of Conneaut Creek, Conneautville Station, Crawford County. Catalogue number 74.336.

FIG. 7. *Cambarus obscurus* Hagen. Left first pleopod of male. $\frac{3}{1}$.

7*a*. Inner view, male, first form. Collected by the writer, Aug. 24, 1904, in the Ohio River, Ambridge, Beaver County. Catalogue number 74.401.

7*b*. Posterior view of same (horny tip of outer part hidden behind inner part).

7*c*. Inner view, male, second form. Collected by the writer, June 24, 1904, in the Loyalhanna River, Crisp, Westmoreland County. Catalogue number 74.352.

7*d*. Inner view, hermaphroditic specimen (type of male, first form). Collected by Atkinson, Graf, and Williamson, May 14, 1899, in the Ohio River, Neville Island, Allegheny County. Catalogue number 7.436. (See text, p. 376.)

7*e*. Posterior view of same.

FIG. 8. *Cambarus bartoni* (Fabricius). Inner view of left first pleopod of male, first form. $\frac{3}{1}$. Collected by the writer, Oct. 6, 1905, at Weskit, near Kittanning, Armstrong County. Catalogue number 74.665.

FIG. 9. *Cambarus carolinus* Erichson. Inner view of left first pleopod of male, first form. $\frac{3}{1}$. Collected by the writer, Sept. 7, 1904, at Dunbar, Fayette County. Catalogue number 74.410.

FIG. 10. *Cambarus monongalensis* Ortmann. Inner view of left first pleopod of male, first form (cotype), $\frac{3}{1}$. Collected by the writer, Oct. 10, 1903, at Edgewood Park, Allegheny County. Catalogue number 74.182.

FIG. 11. *Cambarus diogenes* Girard. Inner view of left first pleopod of male, first form. $\frac{3}{1}$. Collected by the writer, September 5, 1904, at Smithfield, Fayette County. Catalogue number 74.406.

PLATE XL.

FIG. 1. *Cambarus obscurus* Hagen. Upper view of right chela of a male, first form, 77 mm. long, natural size. Collected by the writer, Sept. 30, 1905, in the Alleghany River, Twelve-Mile Island, Allegheny County. Catalogue number 74.663.

FIG. 2. *Cambarus bartoni* (Fabricius). Upper view of right chela of a male, first form, 82 mm. long, natural size. Collected by the writer, Nov. 22, 1905, in Fern Hollow, Pittsburgh, Allegheny County. Catalogue number 74.681.

FIG. 3. *Cambarus bartoni robustus* (Girard). Upper view of right chela of a male, first form 98 mm. long, natural size. Collected by the writer, July 11, 1905, at Spartansburg Crawford County. Catalogue number 74.596.

FIG. 4. *Cambarus carolinus* Erichson. Upper view of right chela of a female, 77 mm. long, natural size. Collected by the writer, Oct. 16, 1905, at Dunbar, Fayette County. Catalogue number 74.669.

FIG. 5. *Cambarus monongalensis* Ortmann. Upper view of right chela of female, 71 mm. long, natural size. Collected by the writer at Edgewood Park, Allegheny County, April 4, 1905. Catalogue number 74.495.

FIG. 6. *Cambarus diogenes* Girard. (Eastern form.) Upper view of right chela of a male, first form, 83 mm. long, natural size. Collected by the writer, Sept. 21, 1905, at Ridley Park, Delaware County. Catalogue number 74.654.

FIG. 7. *Cambarus diogenes* Girard. (Western form.) Upper view of right chela of a male, second form, 93 mm. long, natural size. Collected by the writer, April 15, 1905, at Millvalle, Allegheny County. Catalogue number 74.507.

FIG. 8. Burrow of *Cambarus bartoni* (Fabricius). In spring on hillside, west of Spruce Run, Avalon, Allegheny County, opened by the writer, July 2, 1904.

8a. Side view (section); *8b.* Upper view. *mp*, pile of mud consisting of clay, sand, and small stones; *d*, ditch; *x*, place where crawfish, female, 52 mm. long, was found. At *x* springwater was running into the hole in a strong flow, and running out through the hole, over and past the pile of mud into a ditch.

FIG. 9. Burrow of *Cambarus carolinus* Erichson, located in a swampy place in stiff yellow clay, at Listie, Somerset County. Opened by the writer Aug. 12, 1904.

9*a*. Diagram of disposition of piles of mud seen from above. 9*b*. Section of hole along line *A–D*. 9*c*. Section of hole along line *A–B–C*. *A*. Open chimney. *B*. Closed chimney. *D*. Closed chimney, hole filled up a good distance below surface of ground. *C*. Open hole, without pile of mud, situated under the edge of a large flat stone (*s*). *wl*, water level; *x*, place where the crawfish (male, first form, 61 mm. long) was found.

PLATE XLI.

FIG. 1. Burrow of *Cambarus bartoni* (Fabricius). Located in the sand and gravel of the dry bed of a small stream, Edgewood Park, Allegheny County. Opened by the writer, Oct. 10, 1903. *mp*, pile of mud, consisting of mud, sand, and gravel; *s*, large slab of stone, lying imbedded in sand and gravel; *wl*, water level (the stream was dry for long stretches, only here and there pools of water were left); *x*, place where crawfish (female, 63.5 mm. long) was taken.

FIG. 2. Burrow of *Cambarus monongalensis* Ortmann. Located in yellow clay (mixed with humus), at a springy place on the bank of small stream, near Monongahela City, Washington County. Dug out by the writer, June 16, 1904.

2*a*. Diagram of burrow and chimneys, seen from above; 2*b*, section of hole along line *A–B–C*; 2*c*, section of hole along line *C–D–E*. *A*, hole opening laterally, with one-sided pile of mud in front, keeping up the level of water; *B* and *D*, closed chimneys; *C*, open, large, and regular chimney; *wl*, water level; *st*, stream; *x*, places where the old female (mother, 65 mm. long), and ten young (20.5 to 32.5 mm. long) were found. Water, in a weak flow, was running in at *E*, and was running out at *A*.

FIG. 3. Burrow of *Cambarus monongalensis* Ortmann. Located in yellow clay, at a springy place on the bank of a small stream, Edgewood Park, Allegheny County. Dug out by the writer, May 9, 1904. The burrow is of a type similar to the one figured in Fig. 2, but less complex. *a*, hole opening laterally, with one-sided pile of mud keeping up the level of the water; *b*, closed chimney; *wl*, water level; *st*, stream; *x*, place where the crawfish (female, 63 mm. long) was taken.

FIG. 4. Burrow of *Cambarus monongalensis* Ortmann. Located in black muck, at a springy and swampy place at the bottom of the upper part of Fern Hollow, Pittsburgh, Allegheny County, opened by the writer, Oct. 18, 1903. Type of a hole in level ground, with the water near the surface. No adults and only four young were found in this hole, but possibly the hole had additional branches, which were not discovered, the high stage of the water and its icy coldness rendering investigation difficult. About 1.50 m. from this hole another was opened, which contained a female *C. diogenes*. *a*, closed chimney; *b*, one-sided chimney in front of hole opening obliquely; *wl*, water level; *x*, places where young specimens (11.5 to 16.5 mm. long) were found.

FIG. 5. Burrow of *Cambarus diogenes* Girard. Located in stiff blue clay, in a ditch on a roadside, Nine-Mile Run, Pittsburgh, Allegheny County. Opened by the writer, Nov. 5, 1904. The season had been very dry, and not much water was in the hole. Pebbles were lying on the bottom of the hole. *a*, old chimney, leveled down by rain, probably built in spring; *b*, fresh mud, brought up recently (beginning of fall activity); *wl*, water level; *x*, place where the specimen (female, 77 mm. long) was taken.

FIG. 6. Burrow of *Cambarus diogenes* Girard. Located in yellow clay and humus, at a springy and swampy place in woods on the side of a wagon road, upon which water was standing (after a heavy thunder-shower on the previous day), at Squaw Run, Allegheny County. Dug out by the writer, May 27, 1904. *a*, chimney, consisting of yellow clay; *b*, "stopper" in the mouth of the chimney, distinctly differing from the chimney, the material being yellow clay mixed with blackish mud and leaf-mould; *wl*, water level; *r*, road, with mud-puddle upon it; *x*, place where the crawfish (male, first form, 76 mm. long) was found.

FIG. 7. Burrow of *Cambarus diogenes* Girard. Located in yellow and blue clay, on the border of a swampy place, Schenley Farm, Pittsburgh, Allegheny County. After a sketch furnished by Mr. F. E. Kelly, Nov. 14, 1904. *sw*, swamp; *bc*, blue clay; *yc*, yellow clay; *a*, one-sided chimney, consisting of yellow clay (probably made in spring and summer); *b*, new chimney, consisting of blue clay (fall activity, reclaiming of old burrow at *c*); *c*, old burrow, filled in (during summer) with blue clay, taken or washed in from near the mouth of the lower entrance (*a*) of burrow; *wl*, water level; *x*, place where the crawfish was taken.

FIG. 8. Burrow of *Cambarus diogenes* Girard. Located in blue and yellow clay on the bank of a small stream, Schenley Farm, Pittsburg, Allegheny County. After a sketch drawn by Mr. F. E. Kelly, Nov. 15, 1904. *s*, stream; *bc*, blue clay; *yc*, yellow clay; *a*, new chimney, consisting of yellow clay, evidently coming from the newly dug shaft going down vertically; *b*, upper end of ascending branch of hole, without opening (possibly originally open, but sealed up, and the pile of mud overgrown and obliterated by vegetation); *wl*, water level; *x*, place where the crawfish was taken.

The chimney at *a* shows fall activity, and the vertical shaft is being built by the crawfish in order to get deeper down into the ground.

PLATE XLII.

FIG. 1. Preglacial Monongahela River, after Leverett (1902, p. 89, fig. 1).

FIG. 2. Present range of *Cambarus obscurus* Hagen and *C. propinquus* Girard. (Including variety *sanborni* (Faxon)).

FIG. 3. Distribution of *Cambarus propinquus* Girard, *propinquus sanborni* (Faxon), and *C. obscurus* Hagen.

(For further explanation, see legend on map, and text, p. 433–446).

PLATE XLIII.

Map of Pennsylvania, showing distributional areas of crawfishes. (See Legend on map, and text, p. 465–466).

CONTENTS.

PAGE.

I. INTRODUCTION: SCOPE OF WORK; METHODS; ACKNOWLEDGMENTS 343

II. HISTORICAL REVIEW OF OUR SYSTEMATIC KNOWLEDGE OF THE CRAWFISHES OF PENNSYLVANIA 348

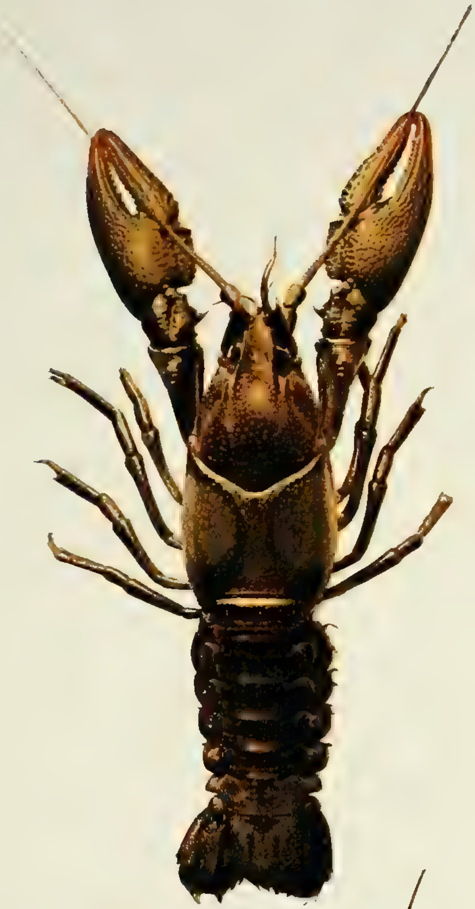
III. MORPHOLOGY AND CHOROLOGY OF THE PENNSYLVANIA SPECIES 350

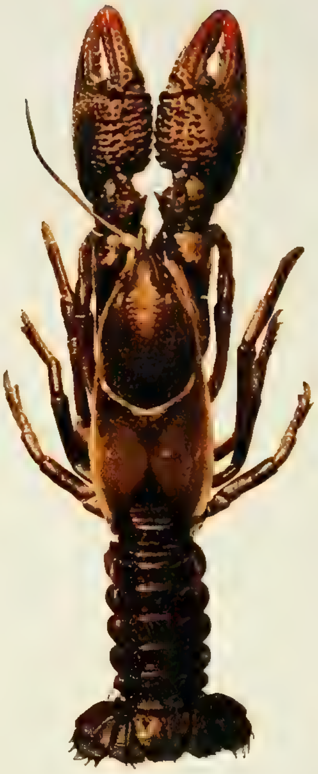
- *A.* General Remarks 350
- *B.* Key for the Pennsylvania species 351
- *C.* Description and Distribution of the species 352
  - 1. Cambarus (Faxonius) limosus (Raf.) 352
  - 2. Cambarus (Faxonius) propinquus Gir. 358
    - 2*a*. Cambarus (Faxonius) propinquus sanborni (Fax.) (extralimital) 365
  - 3. Cambarus (Faxonius) obscurus Hag. 369
  - 4. Cambarus (Bartonius) bartoni (F.) 377
    - 4*a*. Cambarus (Bartonius) bartoni robustus (Gir.) 388
  - 5. Cambarus (Bartonius) carolinus Er. 394
  - 6. Cambarus (Bartonius) monongalensis Ortm. 398
  - 7. Cambarus (Bartonius) diogenes Gir. 402

IV. ECOLOGY AND GEOGRAPHICAL DISTRIBUTION 410

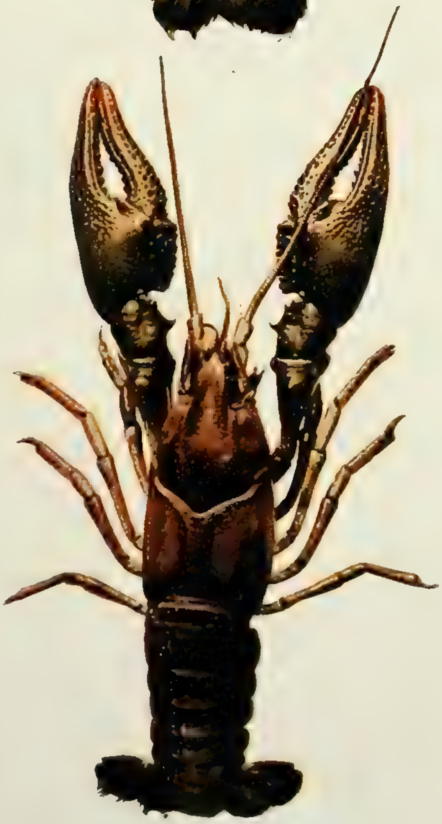
- *A.* Ecology 410
  - 1. The River-Species: C. limosus, propinquus, obscurus 410
  - 2. The Mountain-Stream Species: C. bartoni 413
  - 3. The Burrowing Species: C. carolinus, monongalensis, diogenes 416
    - *a*. General Habitat 416
    - *b*. Shape of Burrows 418
    - *c*. Construction of Burrows 419
- *B.* Geographical Distribution 425
  - 1. Cambarus limosus 425
    - *a*. Summary of facts 425
    - *b*. Origin of distribution 425
  - 2. Cambarus propinquus, sanborni, and obscurus 433
    - *a*. Summary of facts 433
    - *b*. Origin of distribution 434
  - 3. Cambarus bartoni 447
    - *a*. Summary of facts 447

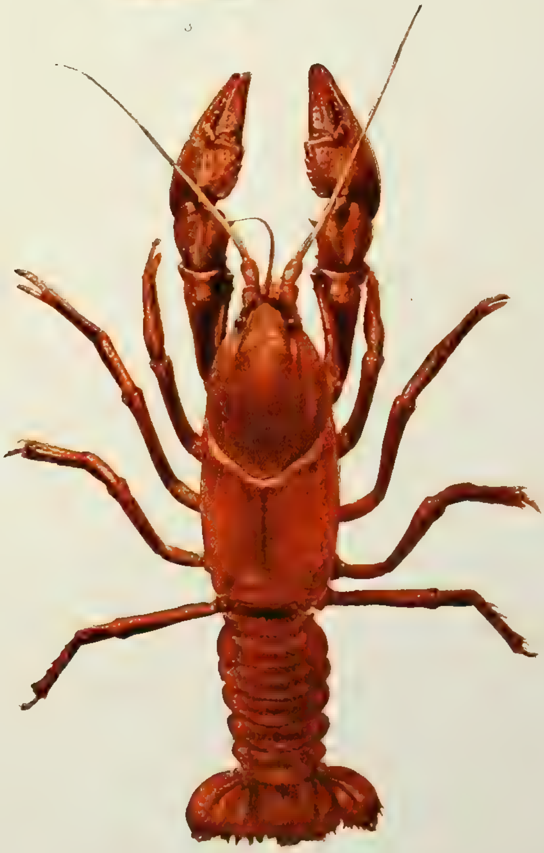
PAGE.
b. Origin of distribution 447
4. Cambarus bartoni robustus 449
a. Summary of facts 449
b. Origin of distribution 449
5. Cambarus carolinus 451
a. Summary of facts 451
b. Origin of distribution 452
6. Cambarus monongalensis 453
a. Summary of facts 453
b. Origin of distribution 454
7. Cambarus diogenes 457
a. Summary of facts 457
b. Origin of distribution 459
8. Summary of studies on distribution 462
V. LIFE HISTORY 469
1. Cambarus obscurus 470
2. Cambarus propinquus and C. propinquus sanborni 476
3. Cambarus limosus 477
4. Cambarus diogenes 480
5. Cambarus bartoni and C. bartoni robustus 486
6. Cambarus carolinus and monongalensis 489
VI. ECONOMIC VALUE 492
1. Popular knowledge of crawfishes 492
2. The use of crawfishes as food and bait 493
3. Crawfishes as scavengers; their food; their enemies 494
4. Crawfishes as obnoxious creatures 496
VII. BEARING OF THE ABOVE STUDIES ON THE THEORY OF EVOLUTION 497
1. The Mutation-Theory of De Vries 498
2. Species, Varieties, and Variations among the Pennsylvania Crawfishes 498
3. Formation of Species by Isolation, as exemplified by Pennsylvania Crawfishes. 504
BIBLIOGRAPHY 513
EXPLANATION OF PLATES 518





3

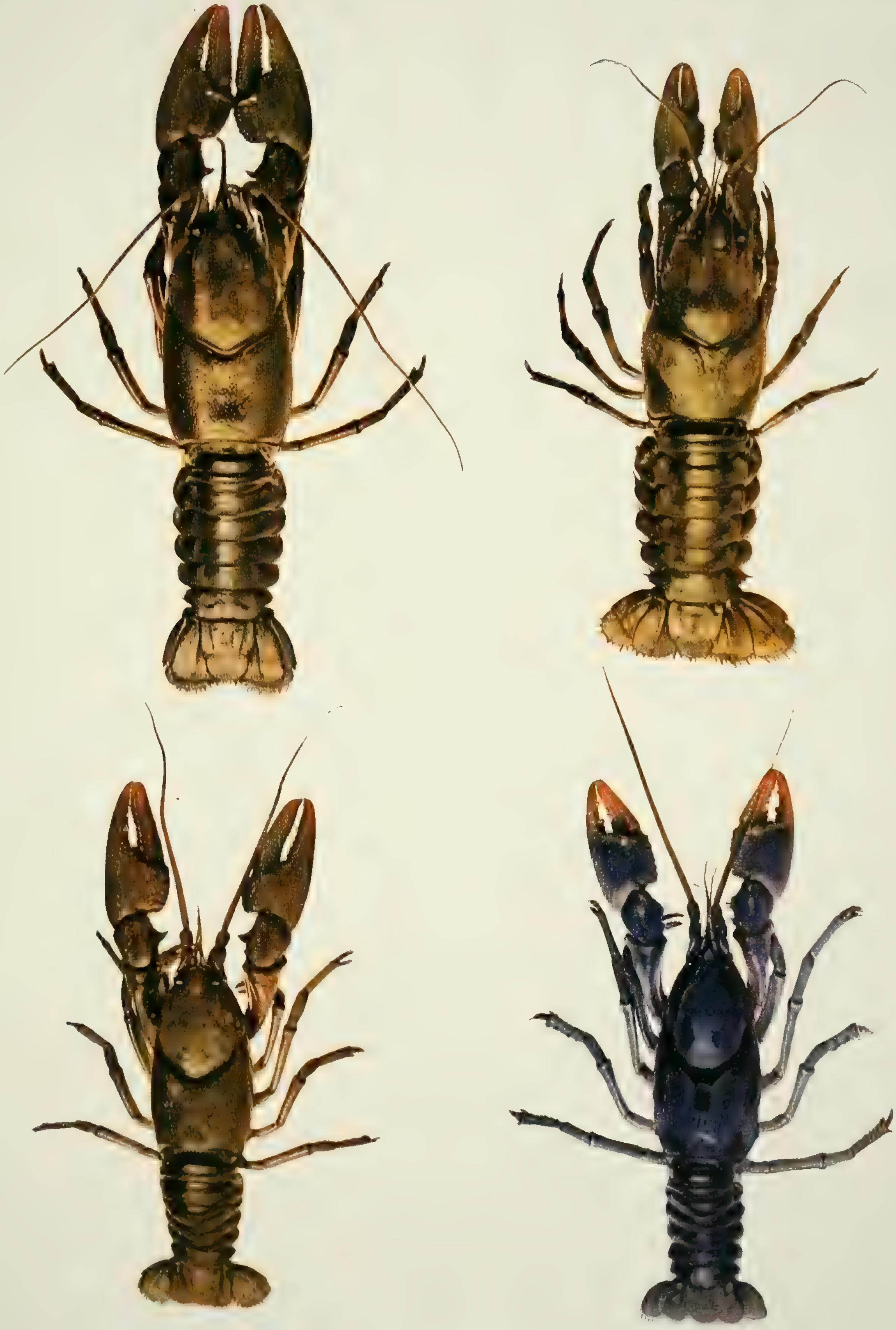




4.

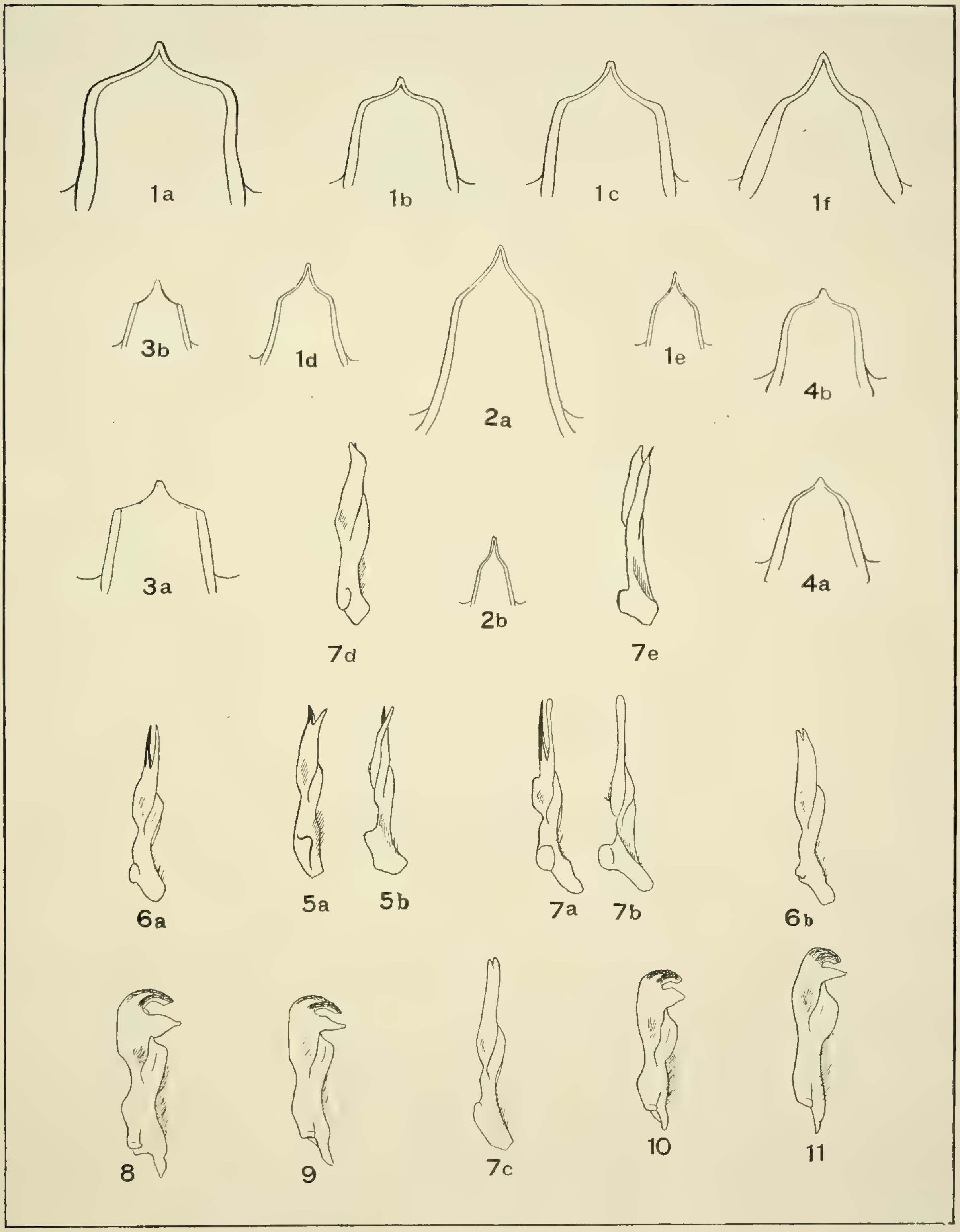
[illegible] CAMBARUS [illegible] HAGEN. CAMBARUS DIOGENES GIRARD.

ZEESE-WILKINSON CO. N. Y.

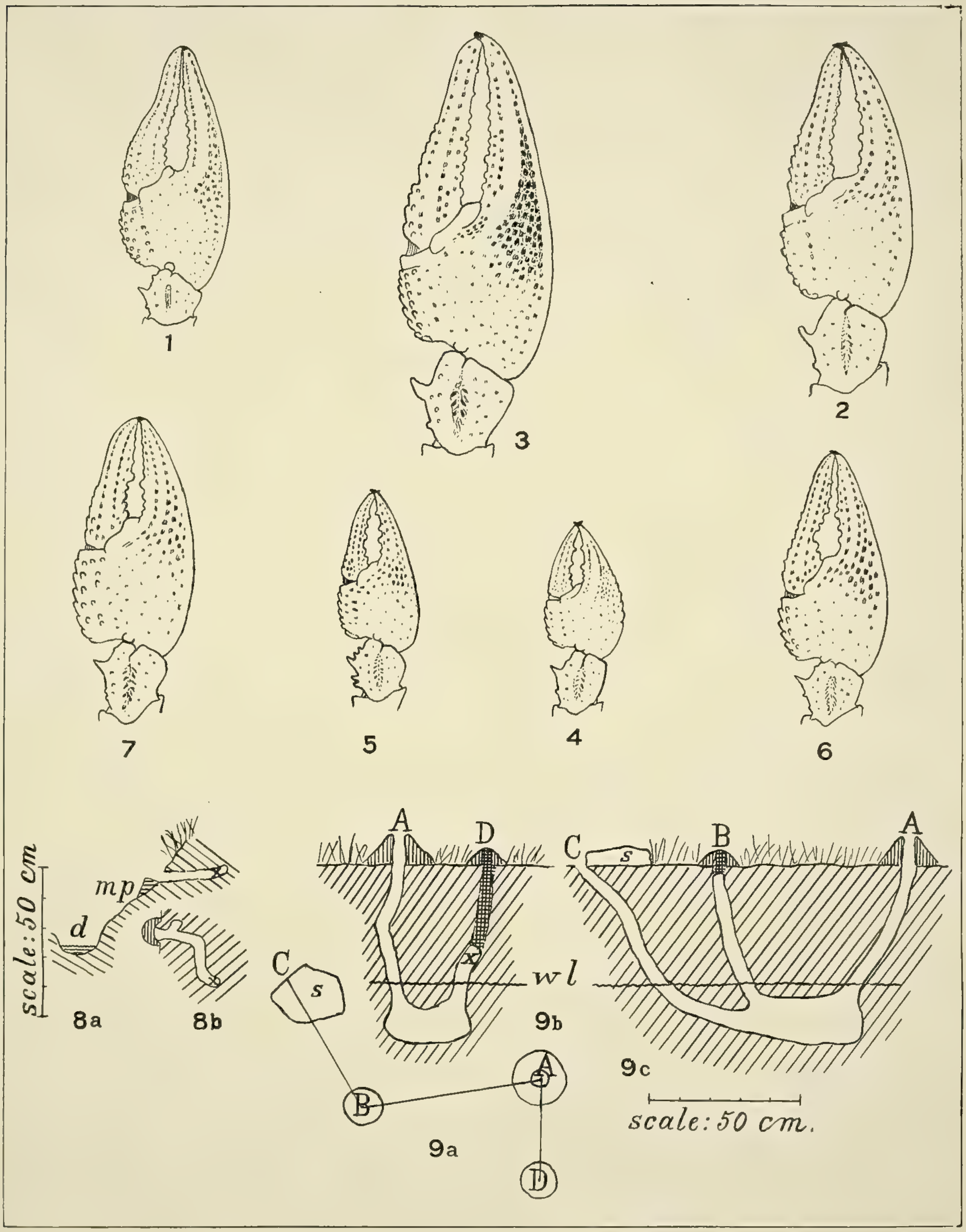


[illegible] [illegible]

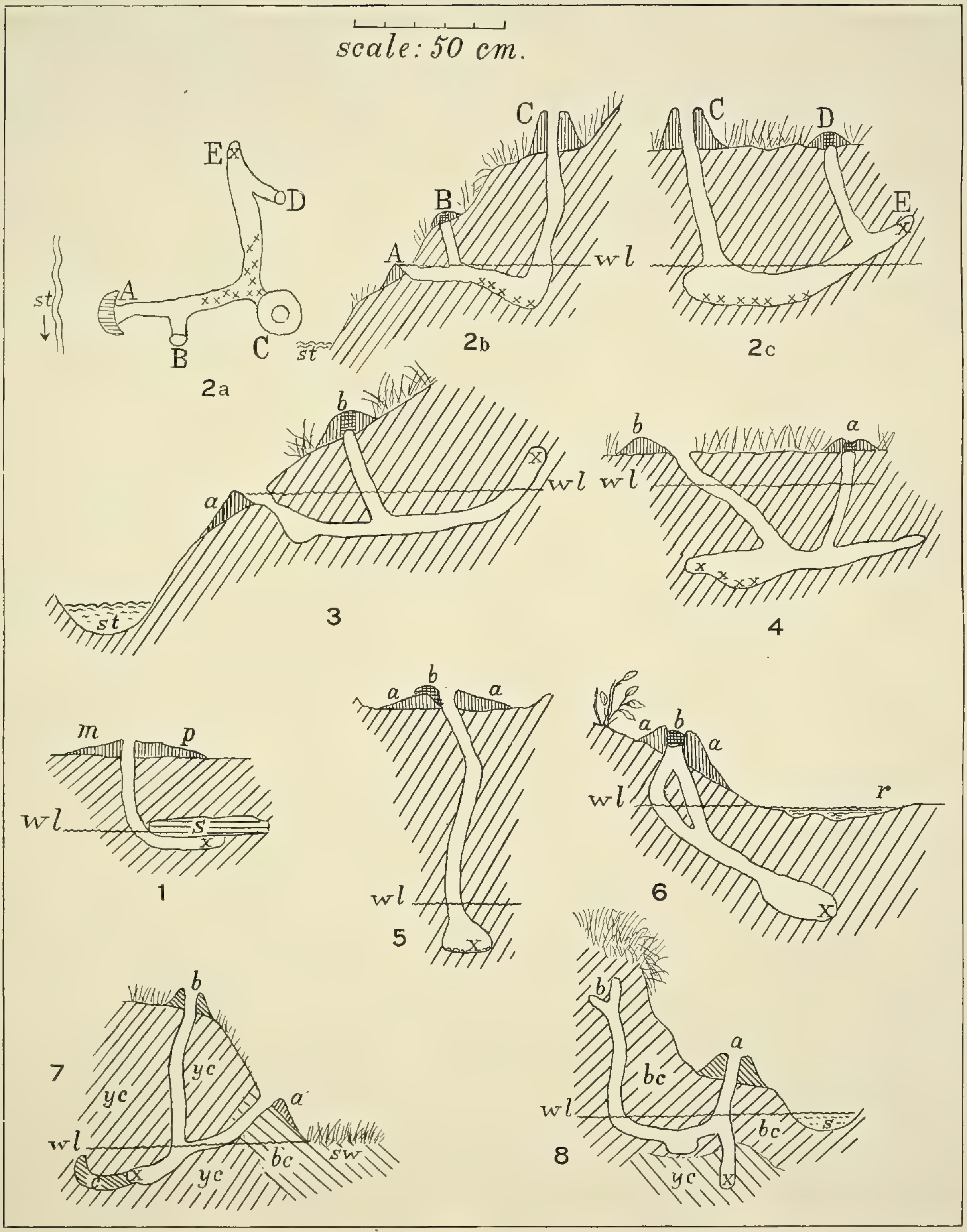
ZEESE-WILKINSON CO. N.Y.



MORPHOLOGICAL DETAILS OF GENUS *Cambarus*.



CHELÆ OF *Cambarus*, FIGS. 1–7. BURROWS OF *Cambarus*, FIGS. 8–9.



Burrows of *Cambarus*.

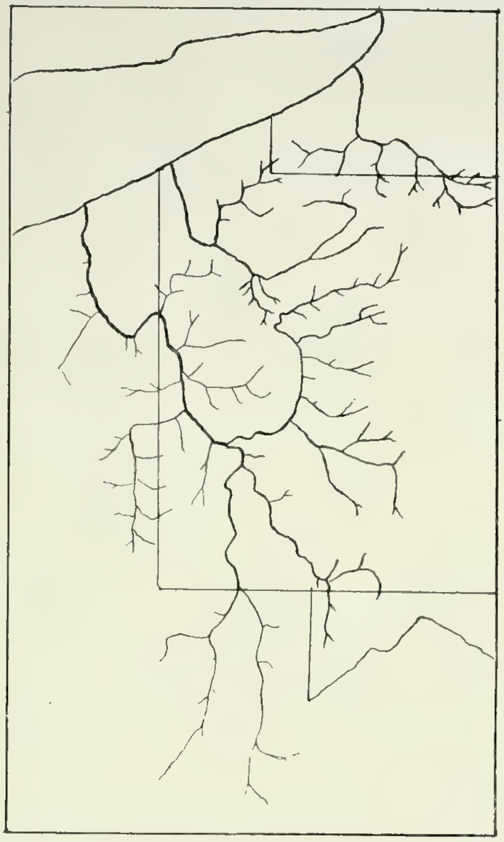


Fig 1 Preglacial Monongahela

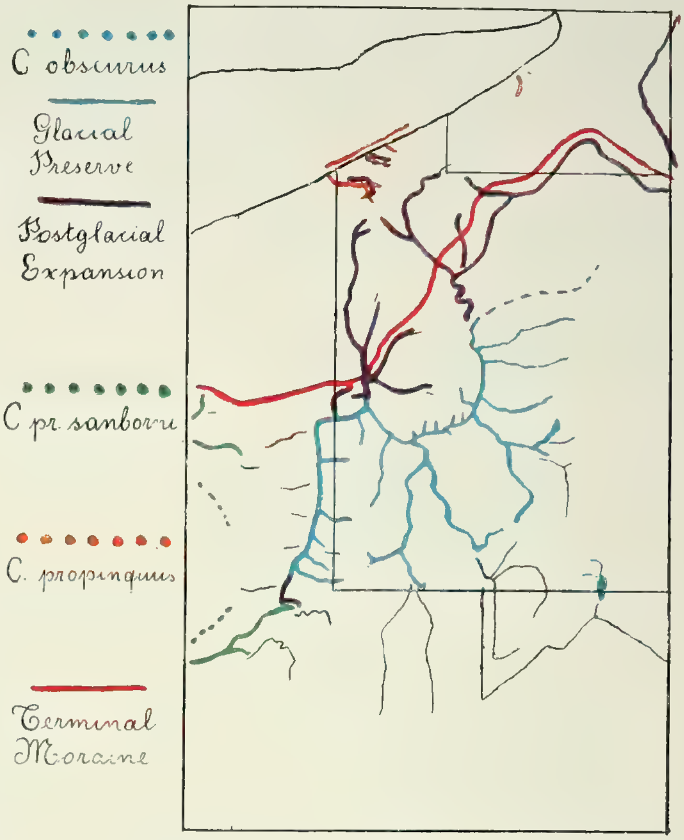


Fig. 2. Range of C. obscurus & propinquus

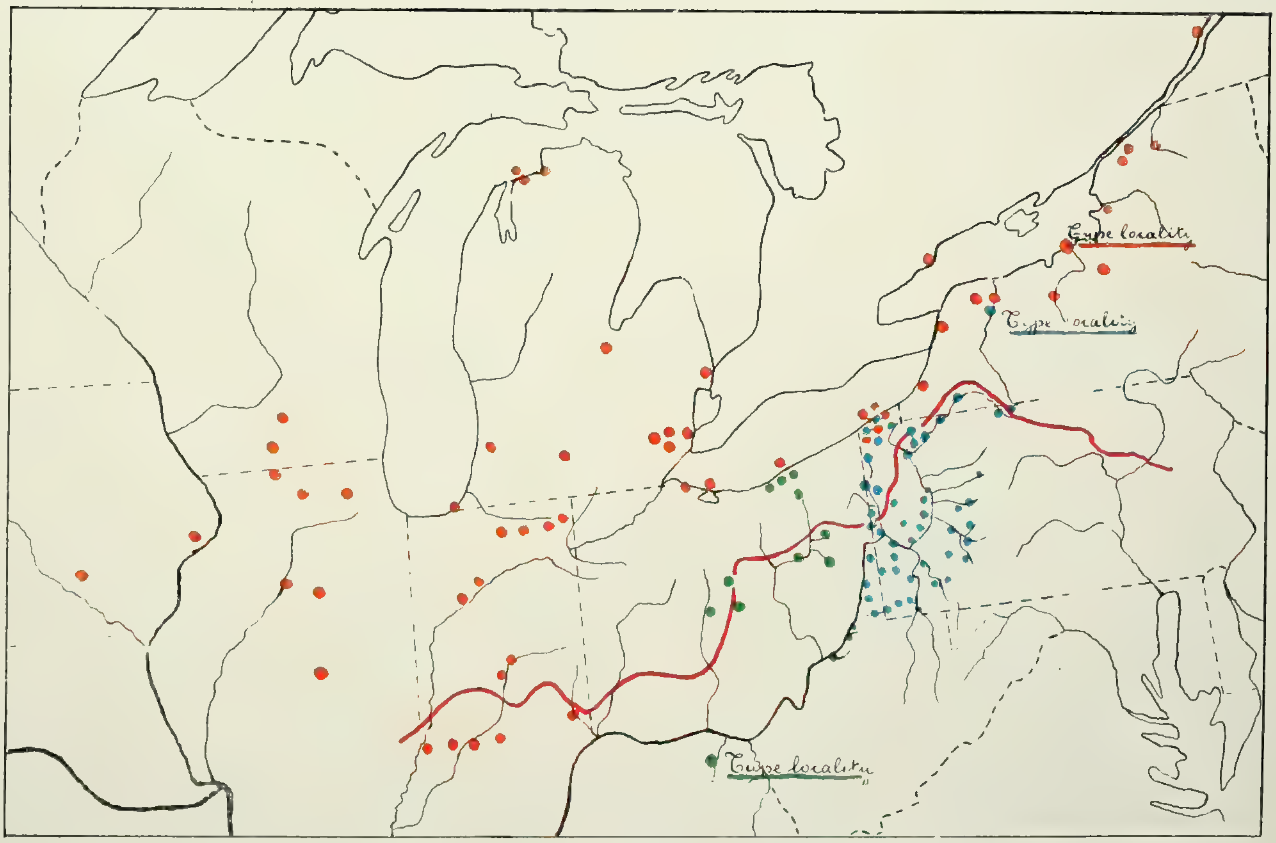
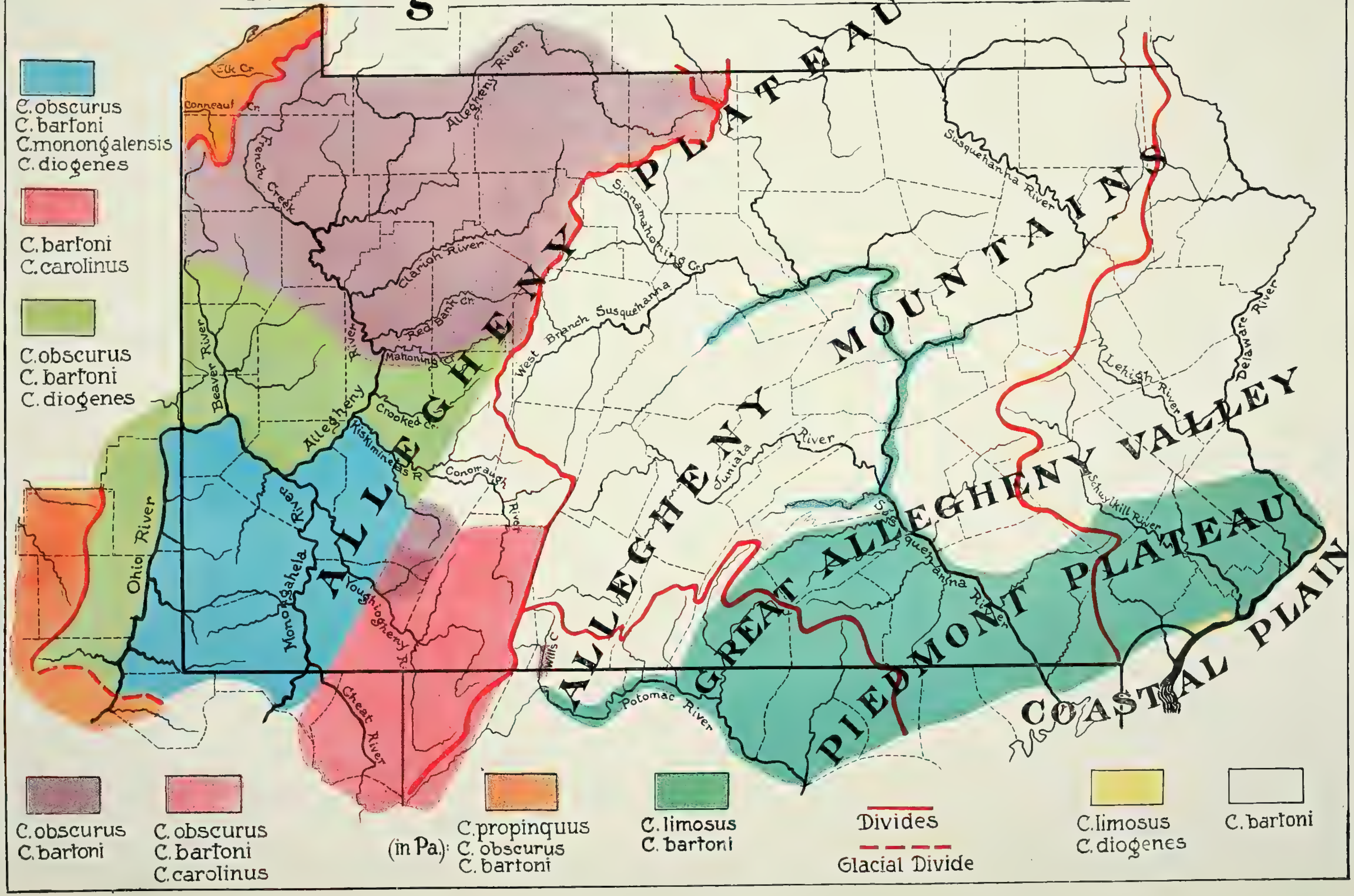


Fig. 3. Distribution of C. propinquus, propinquus sanborni, obscurus

MAP OF PENNSYLVANIA,
showing distribution of crawfishes



INDEX.

(A separate table of contents is provided for the article on the "The Crawfishes of the State of Pennsylvania" by Dr. A. E. Ortmann on p. 523.)

Abbott, J. DeB., 419
Academy of Natural Sciences of Philadelphia, 347
Aceratherium, 174
Acichelys, 290
Additional Remarks on Diplodocus, 72–75
Agate Spring Stock Farm, Sioux Co., Nebraska, 316
Agriculture, Department of, Harrisburg, 348
Agriochœrus, 205, 211
  minimus, 220
Albion, Erie County, Pennsylvania, 361
Alleghany County, Maryland, 344
Allosaurus, 57.
American Jurassic Ichthyosaurians, 325
Amiopsis dartoni, 80
Andrews, Dr. C. W., 225, 244, 259
Apatosaurus, 14
Aplodontia, 142, 143, 144, 148, 149, 151–153, 156–165, 178, 181–184
  rufa, 139, 142
Archelon, 280, 284, 290
  ischyros, 280
Astacidæ, 350
Astacinæ, 350
Astacus affinis, 348, 352, 377
  bartoni, 348, 352, 377
  (cambarus) carolinus, 394
  ciliaris, 377
  fossor, 348
  limosus, 348, 352
  pusillus, 377
Astarte packardi, 79
Atkinson, Dr. D. A., 413, 416, 450 473, 476, 485
Atlantosauridæ, 49
Atlantosaurus, 14, 232
Atlantosaurus, beds, 63, 64, 68–70, 72, 78, 80
Aux Plains River, Illinois, 363

Bad Lands, White River, Dakota, 212
Baptanodon Beds, 70, 78, 80, 81, 336, 337
Baptonodon, 126–128
  discus, 78–80, 82, 84, 98–106, 108, 113, 114, 118, 121, 123, 330, 332, 335, 336, 338, 340, 342
  marshi, 79, 103–105, 110, 113, 114, 119, 121–123, 330, 331
  natans, 78, 79, 117–121, 327, 331
  robustus, 330–334
Barbour, Dr. E. H., 62, 63, 185
Bartonius, 350, 351
Battle Creek, Michigan, 363
Bauer, Franz, 82
Baur, Dr. George, 44, 86, 127
Bayet Collection, 133
Belemnites densus, 79
Benton Beds, 337
  Cretaceous, 336
Beecher, Dr. C. E., 78
Beulah Shales, 67
Bighole River, 209, 211
Big Horn Mountains, Wyoming, 62
Black Tail Deer Creek, Montana, 176
Bothriospondylus, 51, 55
Bothrolabis, 305, 308
  trichænus, 306
Boulenger, Dr. G. A., 225
Brachiosaurus, 15
Brachylophus fasciatus, 254
Braeburn, Pennsylvania, 380
Brontosaurus, 14, 17, 18, 23, 25, 27, 34, 39, 46, 49, 75, 255, 263

Brontosaurus excelsus Marsh, 7, 15
Bunotheria, 213

Camarasaurus, 65, 68
  supremus, 65
Cambarellus, 350
Cambarus bartoni, Description of, 377
    Distribution of, 381
    Remarks on, 386
  carolinus, Description of, 394
    Distribution of, 396
    Remarks on, 397
  diogenes, Description of, 402
    Distribution of, 405
    Remarks on, 407
  limosus, Description of, 352
    Distribution of, 356–358
    Remarks on, 358
  monongalensis, Description of, 398
    Distribution of, 400
    Remarks on, 401
  obscurus, Description of, 369
    Distribution of, 372
    Remarks on, 374
  propinquus, Description of, 358–362
    Distribution of, 362–363
    Remarks on, 364–365
  robustus, Description of, 388
    Distribution of, 390
    Remarks on, 391
  Key to the Pennsylvanian species of, 351
  bartoni, 344, 349, 393, 413–415, 418–440, 443, 451, 452, 465, 466, 469, 476, 486–490, 493, 494, 496, 508–512
  bartoni robustus, 349, 351, 377, 388, 393, 416, 518–520
    diogenes, 352, 402, 416, 509–511, 518, 522
    monongalensis, 351, 398, 510–512, 518–521
    blandingi, 431, 469
  carolinus, 346, 394, 404, 416, 419, 420, 451, 452, 457, 464–466, 489, 495–497, 500–502
  diogenes, 349, 414, 415–420, 423, 424, 453–463, 465, 480–485, 489, 490, 497, 500, 501
  dubius, 349, 394, 398, 402
  indianensis, 503
  limosus, 344, 351, 352, 380, 410, 415, 425, 426–432, 445, 461, 463, 464, 467, 469, 470, 473, 475–478, 481, 486, 492, 499, 501, 503, 505, 509, 519
  monongalensis, 346, 349, 414, 416, 417, 419, 420, 423, 424, 453–461, 465, 466, 489–492, 495, 497, 500, 501, 503, 509–512, 518–521
  montanus, 377
  obesus, 402, 501
  obscurus, 349, 351, 361, 362, 366, 368, 369, 380, 410, 412, 433–448, 463–468, 470, 474, 477–485, 489, 492, 495, 499, 502, 505–509, 512, 518–520
  pealei, 352
  pilosus, 419
  propinquus, 349, 350, 351, 358, 359, 366, 368–371, 380, 410, 433, 434, 436, 438, 439, 441, 442, 445, 465, 476, 492, 499, 501, 505–507, 509, 512, 519
  propinquus sanborni, 350, 365, 368, 433, 434, 436, 439, 446, 476, 477, 492, 499, 505, 506, 507, 522
  robustus, 450, 500
  rusticus, 349, 369, 438, 466, 508
Camden County, New Jersey, 344
Camptosaurus, 293
Canidæ, 179
Canis, 174
Cañon Ferry, Montana, 212
Canyon City, Colorado, 4, 5, 6, 13, 57, 58, 61, 63
Cardioceras cardiformis, 79
Cardiodontidæ, 49
Carnegie, Andrew, 2, 133, 226, 264
Carroll County, Ohio, 344, 367
Castor, 139, 143, 144, 145, 152, 153, 156, 157
  canadensis, 153, 176
  fiber, 144, 145
Ceratogaulus rhinocerus, 179, 181
Ceratosaurus, 57

Cetiosauria, 47, 48, 55
Cetiosaurus, 52, 53
  leedsi, 254
  longus, 52
Chelone, 289, 294
Cheloniidæ, 280, 296
Chelonoidea, 296
Chelydra, 290, 294
Chondrosteosaurus, 50
  gigas, 50
Cimoliosaurus laramiensis, 79
Cockerell, Professor T. D. A., 407
Coggeshall, A. S., 78, 140, 226
Coggeshall, L. S., 3
Colodon, 211
Colpochelys, 290, 293, 295
  kempi, 294
Como Beds, 67
Comptonectes bellistriata, 79
  extenuata, 79
Conotton Creek, Ohio, 367
Cook, Harold J., Jr., 316
Cope, E. D., 59, 66, 68, 82, 86, 127, 173, 174, 185, 213, 305, 310
Cosoryx, 174
  teres, 174
Coturnix novæ-zelandiæ, 133
Crawfishes as obnoxious creatures, 496, 497
  as scavengers, 494–496
  Bearing of the study of, on the theory of evolution, 497
  Bibliography of, 513–517
  Collectors of, 347, 348
  Ecology and Geographical Distribution of Pennsylvanian species of, 410–469
  Economic value of, 492–497
  enemies of, 494
  food of, 494
  formation of species by isolation, 504
  life history of the Pennsylvanian species of, 469–492
  morphology and chorology of the Pennsylvanian species of, 350–410
  mountain stream species, 413
  historical review of our systematic knowledge of, 348–350
Crawfishes of the State of Pennsylvania, Arnold E. Ortmann, 343
  Popular knowledge of, 492–493
  river species, 410
  species, varieties, and variations among the Pennsylvanian, 498–504
  the use of, as food and bait, 493–494
Crocodilia, 47
Cruikshank, Dr. O. T., 450
Cryptobranchus allegheniensis, 495
Cryptoclidus, 260
  oxoniensis, 259
Cryptodira, 295
Cuvier, R., 82
Cylindrodon, 211
Cynomys, 151–154, 156–170, 178, 181
  ludovicianus, 139

Dæmonelix, 139, 177, 185–190, 202
Davison, Professor A. E., 425
Dentalium subquadratus, 79
Dermochelydidæ, 296
Dermochelys, 286, 288, 290, 293
  coriacea, 304
Derry, Pennsylvania, 380
Description of New Rodents and Discussion of the Origin of Dæmonelix, 139–191
Desmatochelydinæ, 296
De Vries, Hugo, 503
  Mutation theory of, 498
Dianthera americana, 412
Dicotyles tajacu, 309, 311
Didelphys, 213
Dinosauria, 5, 20, 44, 45, 46, 47, 74
Diplodocidæ, 49
Diplodocus, 5, 6, 9, 14, 17, 23, 25, 27, 34, 35, 39, 45, 46, 49, 55, 57, 59, 73, 75, 226, 227, 233, 235, 236, 239, 245, 246, 249, 264
  carnegiei, 7, 11, 15, 18, 40, 74, 75, 228, 250
  longus, 75, 251
  vases, 264
Diprodontia, 48
Dogtown Mine, Montana, 212
Dolichorhynchops osborni, 85

Dollo, M., 295
Douglass, Earl, 139, 213
        Tertiary of Montana, 204–223

Eastman, C. R., Fossil Avian Remains from Armissan, 131–138
Echidna, 208
Edward VII., King of England, 226
Elotherium, 209
Entoptychus, 182
Eosphargis, 296
Eretmochelys, 286, 290, 295.
Euhapsis platyceps, 179–183
Eumys loxodon, 174
Eutheria, 208
Eutherian Mammalia, 48
Exposition Society of Western Pennsylvania, 226

Faxonius, 350, 351
Felch, M. P., 5
Fern Hollow, Pittsburgh, Pennsylvania, 388
Filholornis, 131
    debilis, 132
    gravis, 132
    paradoxa, 132
Fishing Creek, West Virginia, 368
Fort Pierre Cretaceous, 284
Fort Union Beds, 67
Fossil Avian Remains from Armissan, 131–138
Fowler, H. W., 478
Francolinus pictus, 133
Frass, E., 82, 127
Freeze Out Hills, 69, 71
Freeze Out Mountains, Carbon Co., Wyoming, 325

Galinsoga, 494
Gallia narbonensis, 134
Gallinuloides wyomingensis, 132
Gallus, 131
    æsculapi, 133
    brayardi, 133
    sp., 133
Garden Park, Colorado, 5
Geomyidæ, 181
Gera, H., 478
Gidley, J. W., 225, 239
Gill, Dr. Theodore, 225
Gilmore, C. W., 71, 72, 98, 116, 127, 225, 239, 336
Gilmore, Charles W., Notes on Osteology of Baptanodon, 325–337
    Osteology of Baptanodon (Marsh), 77–129
Goniomya montanensis, 79
Grammatodon inornatus, 79
Great Oolite, 52, 71
Green River, Edmonson County, Kentucky, 363
Green River limestone, Wyoming, 131
Grim, J., Jr., 308
Gryphæa nebrascensis, 79

Hackberry Creek, Gove Co., Kansas, 282
Hallopus Beds, 78
Hancock County, West Virginia, 344
Haplocanthosauridæ, 54
Haplocanthosaurus, 2, 5, 6, 14, 17, 21, 24, 39, 40, 44, 45, 46, 48–54
    priscus, 4, 6, 10, 22, 27, 28, 32, 34, 35, 38, 43, 49, 54, 75
    utterbacki, 4, 11, 27, 28, 36, 39, 42, 43, 49–51, 54, 75
Harrison Beds, 139, 202, 308
Harrison County, Ohio, 344
Hatcher, J. B., 77, 78, 79, 81, 127, 204, 225-227, 246–252, 255–257, 260–263, 306, 320
Hatcher, J. B., Additional Remarks on Diplodocus, 72–75
    Osteology of Haplocanthosaurus, with Description of a New Species, and remarks on the probable habits of the Sauropods and the Age and Origin of the Atlantosaurus Beds, 1–72
Heer, Oswald, 185
Helodermoides, 205, 211
Hendley H. W., 325
Hesperomys loxodon, 174
Hippotherium, 174
Hoactzin, 131
Holland, Dr. W. J., 133, 140, 204, 281, 320, 325, 348

Holland, Dr. W. J., Osteology of Diplodocus Marsh, With Special Reference to the Restoration of the Skeleton of Diplodocus Carnegiei Hatcher, Presented by Mr. Andrew Carnegie to the British Museum, 225–264
Hollidays Cove, Hancock Co., West Wirginia, 387
Hulke, J. W., 127
Hyænodon, 205, 211
Hyotherium, 305
Hyracodon, 205, 211

Ichthyopterygia, 82, 126–128
Ichthyosaurus, 82, 84, 85–87, 94, 98, 99, 116–118
  campylodon, 124
  communis, 90
  longifrons, 86, 103
  quadriscissus, 86, 89, 92
Ictops, 210, 211
  acutidens, 213, 214, 218, 222–224
  bicuspis, 213
  bullatus, 214
  dakotensis, 212, 214, 223
  didelphoides, 213
  intermedius, 217
  major, 205, 219–224
  montanus, 214, 217–224
  tenuis, 217–221, 224
  thompsoni, 214, 219, 222, 223
Iguana tuberculata, 20254
Iguanodon, 246
  bernissartensis, 244
Insectivores, 208
Ischyromys, 205, 211

James, Joseph T., 185
Jennings, O. E., 140, 441
  Notes on the Vegetable Tissues in Dæmonelix, 190–191
John Day Formation, 183, 305, 306, 310, 319, 320
Jurassic, 45, 46, 61, 64, 117, 325
  of Colorado, 6
  fossils, 79
Jurassic, of North America, 77

Kelly, F. E., 423, 482
King Edward VII., 226
Kinzer, Miss Grace, 488
Kirtlington Station, England
Knight, Wilbur C., 69, 78, 80, 118–121, 127, 332

Lafayette College, Easton, Pennsylvania, 347.
Lagopus albus, 133
  mutus, 133
Lake Douglass, Michigan, 363
Lankester, E. Ray, 410
Leeds, C., 125
Leidy, Joseph, 77
Leptictidæ, of the Lower White River Beds, 208, 210
Leptictis, 213
  haydeni, 212, 214
Lesley, J. P., 279
Lima sp., 79
Limnenetes, 205, 211
  anceps, 220
  platyceps, 220
Linesville, Crawford County, Pennsylvania, 440
Lingula brevirostris, 79
Little Medicine Bow, Wyoming, 6
Loomis, Dr. F. B., 79, 127
Loup Fork Miocene, 306
Lower Madison Valley, Montana, 177
Lower Pliocene, 131
Lutra, 261, 263
Lutraria senna, 185
Lydekker, R., 99, 124–127
Lytoloma, 286, 294, 295

Mammoth Cave, Kentucky, 380
Manatee, 56
Marsh, Othniel Charles, 2, 5, 6, 14, 44, 47, 48, 49, 56, 59, 62, 66, 67, 68, 77, 113, 116, 127, 225, 227, 229, 232, 238–243, 250–252, 266, 268, 270, 272
Marshall County, West Virginia, 344
Marsupials, 208, 213
Matthew, Dr. W. D., 78, 225
McCarty's Mountain, 204, 214

McConnell, W. R., 358, 426, 441, 474, 478
Megalneusaurus rex, 79
Megalosauria, 47
Meleagris antiquus, 131, 132
    celer, 133
    superbus, 133
    sp. ind., 133
Menopoma, 19, 51
    allegheniensis, 20
Merriam, Dr. J. C., 98, 104, 128, 332, 336
Merrill, Dr. George P., 225
Merychyus, 174
Mesodectes, 213
Mesohippus, 211
    latidens, 220
Mesoreodon, 139, 179
Metamynodon, 209
Metatheria, 47, 48
Micropterus, 494
Middle Miocene, 131
    Island Creek, West Virginia, 367
    Miocene, 131
Middle White River, 210
Mineral County, West Virginia, 344
Modiola sp., 79
Morgan County, West Virginia, 344
Morosauridæ, 49, 54
Morosaurus, 5, 13, 14, 17, 27, 34, 39, 42, 49
    grandis, 14
Morrison Beds, 67
Multituberculates, 208
Mylagaulidæ, 179
Mylagaulids, 172, 181
Mylagaulus monodon, 179

Natrix sipedon, 495
Necturus maculosus, 495,
New Hagerstown, Ohio, 415
A New Monotreme-Like Mammal, 204
New Suilline Remains from the Miocene of Nebraska, 305–320
Niobrara Cretaceous, 296, 300
Niobrara River, Nebraska, 308
Nopsca, Baron F., 54, 262
Notes on Osteology of Baptanodon, 325–337
Notes on the Vegetable Tissues in Dæmonelix, 190–191

Oberlin College, Ohio, 355
Oil Creek, Colorado, 5
Oligocene, 131
Ophthalmosaurus, 71, 111, 112, 126, 128, 336, 337
    cantabrigiensis, 119, 125, 336
    discus, 121
    icenicus, 119, 120, 123, 336
    natans, 120
Opisthocœlia, 47, 48
Opisthocomus, 131
Oreodon Beds, 209, 210
Ornithopoda, 47
Ornithopsis, 55
Ornithorhynchus, 208
Ortalis, 131
Orthopoda, Cope, 47
Ortmann, Dr. Arnold E., The Crawfishes of the State of Pennsylvania, 343
Osborn, H. F., 18, 55, 67, 69, 72, 225, 227, 228, 244, 247, 252, 253, 255
Osteology of Baptanodon (Marsh), 77–129
Osteology of Diplodocus Marsh, with Special Reference to restoration of Skeleton of Diplodocus Carnegiei Hatcher, Presented by Mr. Andrew Carnegie to the British Museum, 225–264
Osteology of Haplocanthosaurus, with Description of a New Species, and Remarks on the Probable Habits of the Sauropoda and the Age and Origin of the Atlantosaurus Beds, 1–72
Osteology of Protostega, 279–298
Osteopygis, 294
Ostrea engelmanni, 79
Owen, R., 82, 89, 128
Oxydactylus, 139

Palæictops, 213
Palæochœrus, 305
Palæolagus, 211
Palæoperdix, 131
    longipes, 132

Palæoperdix, prisca, 132
    sansaniensis, 132
Palæortyx, 131
    blanchardi, 132
    brevipes, 132
    cayluxensis, 132
    edwardsi, 132
    gallica, 132
    hoffmani, 132
    media, 132
    phasianoides, 132
Palæotetrix gilli, 133
Palæotherium, 209
Panhandle of West Virginia, 372
Pantosaurus striatus, 79
Paracambarus, 350
Parastacinæ, 350
Paris Basin, 131
Paulmier, F. C., 467
Pediocætes lucasii, 133
    nanus, 133
    phasianellus, 133
Penns Manor, Pennsylvania, 355
Pentacrinus asteriscus, 79
Peratherium, 211
Perdix sp., 133
Peterson, O. A., 81, 137
    Description of New Rodents and Discussion of the Origin of Dæmonelix, 139-191
    New Suilline Remains from the Miocene of Nebraska, 305–320
Phacochœrus æthiopicus, 310
Phasianidæ, 135
Phasianus, 131
    altus, 132
    archiaci, 133
    desnoyersi, 132
Philadelphia, Pennsylvania, 344
Pholodomya kingi, 79
Pholidophorus americanus, 80
Piedmont, South Dakota, 6
Pilsbry, H. A., 427
Pinna sp., 79
Pipestone Springs, Montana, 213, 214
Pittsburgh, Pennsylvania, 343, 347
Plates, Explanation of, 129, 138, 194, 196, 198, 200, 202, 224, 518
Platygonus leptorhinus, 308, 310
Pleistocene, 131
Plesiosaurus shirleyensis, 79
Pleurocœlidæ, 49
Pleuromya subcompressa, 79
Polychrus marmoratus, 254
Potamobiidæ, 350
Potamobius, 350
Potomac River, 355
Prairie Dogs, 188, 189
Predentata, 44, 45, 47, 48, 72
Prentice, Sydney, 3, 78, 140, 204, 283, 320
Preston County, West Virginia, 344
Procambarus, 350
Procamelus, 174
Procœlia, 47
Promerycochœrus, 139, 179
Protohippus, 174
Protostega, 290, 292, 293, 294, 295
    gigas, 279–292, 300, 302
Prout, Dr. Hiram, 209
Psephophorus, 296
Pseudomonotis curta, 79
    orbiculata, 79
Purbeck, 72

Quercy Phosphorites, 131

Rathbun, Miss M. J., 350
Red Fork of Powder River, Big Horn Co., Wyoming, 81, 333
Reed, W. H., 123, 325, 329, 336
Rocky Mountains, 23
Rosebud Beds, 174
Rough Run, Butler County, Pennsylvania, 391
Rumex acetosella, 494

Sauranodon, 117
Sauropoda, 16, 19, 21, 24, 39, 40, 43–47, 49, 51, 55, 57, 59
Sauropterygia, 259
Schenley Park, Pittsburgh, Pennsylvania
Sciuromorphs, 170
Scott, W. B., 69, 139
Seeley, H. G., 89, 128, 259

Septaria, 79
Shastasaurus, 104, 105, 107
Sinclair, W. J., 305
Smoky Hill River, Kansas, 279
Sphenodon, 92, 245
Spirophyton, 185
Stark County, Ohio, 344
Stegosaurus, 57
Steneofiber barbouri, 166, 167, 169, 171, 175 178, 185, 194, 196
    complexus, 177
    eseri, 144
    fossor, 140, 141–144, 147, 150–154, 156–159, 170, 175, 177, 178–187, 194, 196, 198, 200
    gradatus, 166, 173, 178
    hesperus, 176
    montanus, 157, 162, 175, 176
    nebrascensis, 172
    pansus, 146, 147
    peninsulatus, 144, 145, 172, 175
    platyceps, 194
    viciacensis, 144, 145, 172, 177
Sternberg, Charles, 281
St. Louis Fur Company, 209
St. Mary's Lake, Michigan, 363
Struthio, 263
Surface, H. A., 495
Sus scrofa, 310

Talpa europæa, 189
Tancredia extensa, 79
    inornata, 79
    warrenana, 79
Taonurus, 185
Taoperdix, 131, 134
    keltica, 132, 134, 138
    pessieti, 132, 134–138
Templeton, Pennsylvania, 387
Tertiary of Montana, 204–223
Tetrao pessieti, 134
    tetrix, 133
    urogallus, 133
Theropoda, 44, 45, 46–48, 72
Thinohyus, 305
    brachyceps, 306
Thinohyus, decedens, 318
    lentus 4, 319
    osmonti, 320
    pristinus, 314, 319
    rostratus, 319
    siouxensis, 308, 309, 310, 316, 319, 322, 324
    socialis, 319
    subæquans, 306, 319
Thracia weedi, 79
Three Forks, Montana, 220
Titanotherium, 205, 209, 211, 220
Titanotherium Beds, 204, 213, 214, 217
Todd, W. E. C., 440
Toretocnemus californicus, 332
Torresdale, Pennsylvania, 355
Toxochelys, 281, 288–290, 295
    bauri, 295
    latiremis, 293
Triassic of Colorado, 6
Trigenicus socialis, 220
Trigonias, 209
Troublesome Creek, Carbon Co., Wyoming, 81
Tucker County, West Virginia, 344
Twelve Mile Island, Pennsylvania, 371
Tympanuchus pallidicinctus, 133
Tyranosauridæ, 49

Uinta, 299
Ungulata, 48
Unio, 57
Upper Eocene, 131
Upper John Day, 306, 320
Upper Miocene, 139, 177
Utterback, W. H., 2, 3, 4, 5, 6, 62, 65, 72, 81, 227, 252, 253, 255, 278, 333
Uhler, Dr. P. R., 393, 484

VanKirk, A. W., 3, 140
Varanus niloticus, 254

Warbonnet Creek, Nebraska, 179
Ward, Lester F., 69
Wealden, 71, 72
Weskit, Armstrong County, Pennsylvania, 387
White River Beds, 209, 211, 213

White, Dr. C. A., 59, 63, 69
White River, Indiana, 363
        Oligocene, Colorado, 131
Wieland, G. R., 295
    Osteology of Protostega, 279–298
Williamson, E. B., 376
Wills Creek, Ellerslie, Maryland, 372
Williston, S. W., 69, 85, 116, 123, 128, 280, 292, 293, 336
Woods, J. G., 189
Woodward, Miss Alice B., 229, 230, 254, 259
    Dr. A. S., 82, 124, 225, 254, 256, 259, 264
    Dr. Henry, 230
Wortman, Dr. J. L., 81

Xenotherium, 211
    unicum, 204, 224

526

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 00895 8001